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## FROM THE EDITORS

### Of Reviews, Reviewers, Editors, and Authors

Reviews are commonly viewed by authors as a dreary annoyance. One gives the manuscript a second look a couple of days after final typing. It seems to be perfect. It is mailed in triplicate because journal editors require copies for reviewers. A couple of months later, two much marked copies come back to the chagrined author. In addition, one reviewer has written nearly two pages of commentary and suggestions. An accompanying letter from the editor refers to some of the reviewer suggestions and states conditions under which a revised manuscript will be acceptable for publication.

Author reactions are diverse. Some, swallowing their pride, slavishly try to follow nearly all suggestions. At the other extreme, the displeased author withdraws the manuscript and submits it to another journal. Or he<sup>1</sup> gives up and lets it die in a back file. The preponderance, however, critically consider views and suggestions expressed and note corrections. They commonly initiate negotiation with the editor concerning proposed changes in the manuscript.

Correspondence with the editor is sometimes of a querulous nature, or even if not so, it may be evident that authors view editors myopically and feel that they (the editors) are not able successfully to place themselves in the writer's shoes. Such a premise implies that editors and authors are two different kinds of beings who lack overlapping experience. This is not true. Most journal editors are authors who have published extensively. In fact, their nomination as editors (very few, I suspect, volunteer) usually derives from publication reputation.

But editors are not necessarily writers who have successfully risen above the hazards of publication review. Take this one for example. The last two papers he submitted to disciplinary journals came back for revision. In one case, the editor wanted a long paper reduced to a single topic. In the other instance, a broadening of the scope of a short article was requested. The editor's position in both instances was partially derived from that of the reviewers who also supplied numerous suggestions and some corrections. The author did not agree with all of this, but he was willing to comply with the major changes in content. These required considerable rewriting. Editors are authors and have first-hand experience with the experiences and views of the latter group.

Because of the interdisciplinary nature of the *Iowa State Journal of Research*, the Editor is more dependent upon reviewers than in most journals. But because he does not know the people in fields far from his disciplines, the task of finding competent reviewers can be an arduous procedure. The *Journal* has been successful in obtaining the help of Associate Editors for those fields from which it receives an appreciable number of submissions. The Associate Editors, within their respective baliwicks, monitor the review procedure and make recommendations to the Editor. Otherwise the *Journal* seeks advice from formally designated or informal consultants in the search for competent reviewers.

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<sup>1</sup> An all service pronoun: he, her, his, hers.

There is a considerable difference in the quality of reviewers. Within a restricted field an editor commonly knows people well enough to know (or soon learns) whom to avoid: those who invariably refuse review invitations, those who procrastinate or who never return a paper, those who limit their scrutiny to a superficial scan, and those who use the review privilege as an ego-message. And others. But in disciplines foreign to the Editor and even with consultant help, solicitation of reviews for the *Journal* must commonly be on a hit-and-miss basis. Often we send "Will you review" letters to at least four people in the hope of obtaining a couple of competent reviews within a reasonable length of time.

The personality and vision of reviewers, as above noted, of course color their advice to the editor and the author. If the manuscript is a very poor one, it will probably draw similar remarks from different reviewers. Otherwise, this is usually not the case; reviews of the better papers are commonly mutually exclusive, and perhaps this is a mark of a good paper. Because of these considerations, this Editor in correspondence with authors commonly writes a review of the reviews.

Thus there are inequalities in the review process the editor must consider. But I am constantly amazed (and pleased) that so many individuals are willing to give so much time and careful thought to their anonymous and unrewarded efforts. The manuscript marking and commentary submitted by many reviewers takes literally hours of effort. Both editors and authors owe a considerable debt of gratitude to people who participate in prepublication review.

The *Iowa State Journal of Research*, of necessity, is more permissive than most disciplinary journals in matters of format and manner of presentation. This is because acceptable writing procedure and the structure for literature citation differs widely between cultural fields. But to a greater extent than in disciplinary journals, it could not maintain reasonable standards of publication quality without the help of reviewers.

## EVIDENCE FOR INTERFERENCE WITH NAVIGATION OF HOMING PIGEONS BY A MAGNETIC STORM

P. H. Carr, W. P. Switzer, and W. F. Hollander<sup>1</sup>

**ABSTRACT.** On August 9, 1972, the Ames, Iowa, Racing Pigeon Club flew 70 birds from 55 km west during a moderate-strength magnetic storm, and 50 failed to home. Race reports from other clubs on a previous day of severe magnetic storm, June 17, 1972, indicated interference with east-west homing except in northwestern United States but no interference with north-south homing. It is suggested that the birds detect differences in magnetic intensity as a cue in judging latitude.

Additional index words: Pigeon, Racing pigeon, Homing, Navigation, Magnetic sense, Magnetic storm, and Geomagnetism.

### INTRODUCTION

In the past dozen years convincing evidence has been obtained for some sort of magnetic sense in migrating and homing animals and birds. However, their navigation utilizes a complexity of other cues as well as geomagnetism, and there are technical difficulties in deducing the interplay. The present paper contributes a new kind of data to the subject.

In the spring of 1972 the AME Racing Pigeon Club of Ames, Iowa, asked one of us (PHC) for information concerning the use by racing pigeons of the Earth's magnetic field in their navigation and whether navigation would be degraded by magnetic storms. As we knew nothing of pertinent experiments, the Club agreed to initiate an investigation. The original plan was to have the birds released at a considerable distance from home during magnetic storms and to record the homing performance. Magnetic storms typically develop about 36 hours after emergence of a solar flare directed at Earth; therefore, we obtained cooperation of the Environmental Research Laboratories, National Oceanic and Atmospheric Administration (NOAA) at Boulder, Colorado, to notify us by telephone when a magnetic storm could be expected.

Our first alert came June 17 (a Saturday). NOAA had not observed a solar flare, but a magnetic storm was already in progress—a surprise. Forty birds were sent to Decatur, Nebraska (about 240 km from Ames) and released the next morning (June 18) at 0630 CDT. These birds all returned in good time, being home by noon.

During the summer several more flights of the Ames birds were made during times of predicted magnetic storms, which turned out to be low-level, with some apparent degradation in flight speed in homing but still nothing remarkable. However, on August 9 on a flight of 55 km directed east in good weather, 50 birds out of 70 failed to home. This time the magnetic disturbance was very active by 0400 CDT. Magnetic charts showed the storm decreased rather quickly by the time our birds were in the air. During the flight the

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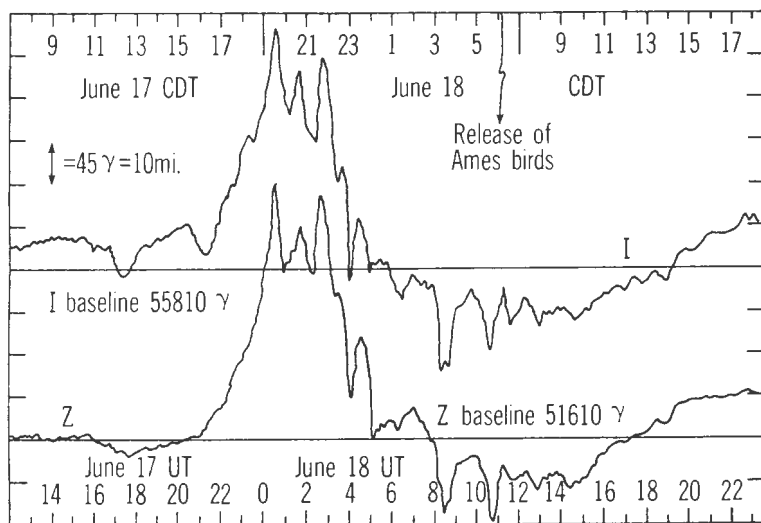


Figure 1. Magnetogram data for June 17-18, 1972, Boulder, Colorado. Digitized every six minutes from original NOAA charts. Z = vertical vector of the magnetic field; I = total magnetic field (instantaneous value). One division on the ordinate = 45 gammas = 10 miles difference in latitude. CDT = Central daylight time. UT = universal time. Before and after the period here included the readings were fairly steady.

storm was moderate in strength (K index 4 to 5). After this serious loss of birds the cooperating club members understandably lost much of their enthusiasm for such investigation, and the tests ended.

The Ames club's rather insignificant results might have been the end of our interest also except for unexpected outside information. On Sunday evening, June 18, the same day that our club had a good return from Decatur, Nebraska, one of us (WPS) learned of a telephone call to a club member from the secretary of the Greater Chicago Combine of Pigeon Racers. The secretary told of a "smash"—the Combine's 500-mile (800 km) race from Norfolk, Nebraska, had started at 0600 CDT, Saturday, June 17, with 1012 birds, and no birds homed that day. Only 39 birds had returned by Sunday night. Furthermore, the Fox Valley Club (not far from Chicago) had also started its 500-mile (800 km) race with a thousand birds at the same time from Fremont, Nebraska, and not a single bird had returned at time of notification. Normally, only seasoned birds are sent on such races, and 70-80 percent are expected back by the end of the second day.

We informed NOAA of the "smash," and they immediately sent photocopies of magnetograms made at Boulder and at Fredericksburg, Virginia, for the pertinent period. These showed that the intense magnetic storm had largely dissipated by Sunday, June 18 (see Fig. 1). We realized then that the Ames

club birds released that day had not confronted the same sort of conditions that the Chicago birds had the previous day. Therefore, it seemed of special interest to learn more about the effects of the magnetic storm of June 17, 1972, on other races in the United States that day.

## METHODS

The immediate objective was an assay of major races held in the United States on June 17, 1972, and comparison with those of the same clubs in the two races immediately before and one race immediately after that date. (The races generally are at weekly intervals.) Race reports are provided in the *Racing Pigeon Bulletin*, a weekly publication (Marcus Hook, PA 19061). These reports give information on the release point, weather, number of birds, and speed of about the best four percent. The number of birds failing to return, unfortunately, is not provided. Thirty-one clubs held major races June 17. The race report information was first transposed into synoptic form for each club. Daily after-the-fact weather maps from the U.S. Weather Bureau and photos from satellites were used to confirm or modify reports from the racers. Unfortunately at that period only one satellite photo per day was available, and that was for early afternoon (U.S.) when the weather was usually best. Magnetic field conditions were also noted; they were normal (no magnetic storms) for all the race dates involved except for June 17.

Comparison of the race performances necessitated some degree of subjective evaluation. To aid in this, two of us (PHC, WPS) acted as independent judges and also enlisted the independent cooperation of Dr. Clayton C. Beegle, then of the Zoology Department, Iowa State University, and an AME club member. Each made a list categorizing each club's performance on the 17th as better than, the same as, or worse than would be expected from the overall record of the club. We had to consider a number of variables in making the judgments; for example, performance on a long race can be expected under normal conditions to be slower than on a shorter one, and releases of large numbers of birds should give better top speeds than with smaller numbers. Wind direction and velocity, and cloud cover are important, as well as topography encountered.

The comparison lists suggested that regional differences would also have to be considered in subsequent analyses. Therefore the races were plotted on a map of the United States (Fig.2). Division into three regional groups seemed useful: the far West, the Midwest, and the East. On June 17, the Western group had eight races, the Midwest nine, and the East fourteen. A further analysis of the comparisons indicated that race direction was important, as explained subsequently. (Unfortunately one club was accidentally omitted in the judging; we do not know which one, but it was in the West.)

## RESULTS

Matrix presentations of the clubs' performances as rated by the judges are presented in Tables 1 and 2. In general, there was fair agreement among the judges, and some very obvious differences between categories are evident. Of particular interest is the fact that no club racing north or south octant on June 17 did worse than expected; also no club in the West region suffered. On the other hand, only one judge considered that an East region club

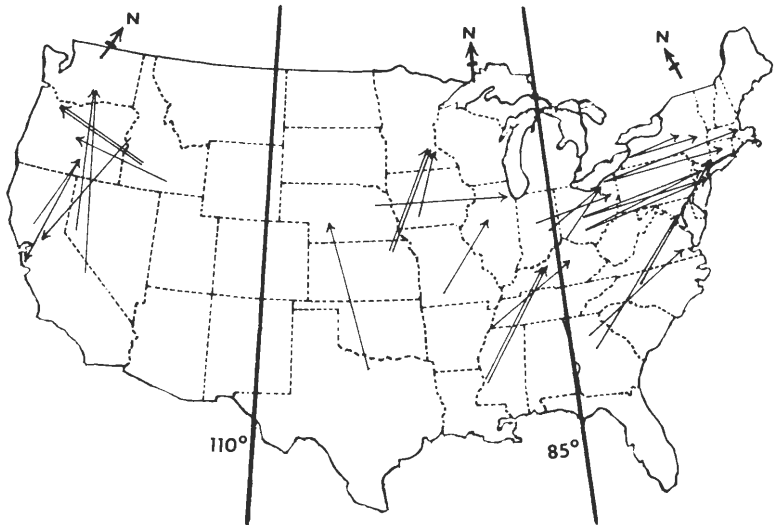


Figure 2. Locations of 31 pigeon races in the United States on June 17, 1972, as reported in *Racing Pigeon Bulletin*. The 85° meridian is the arbitrary division between Eastern and Central, and the 110° meridian between the Central and Western groups. Magnetic north direction is indicated by the cross-bar arrows. Each plain arrow points from the race release to the home location.

performed above expectations on June 17. Flights directed in east or west octants on June 17 were the poorest. Chi-square analysis confirms highly significant differences in the several categories. These results indicate that this magnetic storm did not degrade the navigation of birds flying north or south as compared with those flying east or west. Another implication might be that the birds in the Western region did not rely significantly on geomagnetism for navigation. Perhaps both interpretations are valid.

The fact that there were no Eastern races in a north or south direction, and that no Western race was degraded on June 17 makes it impossible to separate satisfactorily the relations between location of home loft and direction of flight to performance in East and West. If one looks to the Central region for an answer, the evidence is better. Four races on June 17 were directed north (none south) involving 447 birds, of which 30 were reported. One race was judged better than previous races and three were judged as about the same as the previous. There were two races directed east: the 500-mile "smashes" noted in the introduction (but the Fox Valley results were not reported in the *Racing Pigeon Bulletin*). There were four diagonal races, none judged to be better than previous performances, and three judged worse. The Central region lacks great variations in elevation or significant topographical features, in contrast with either East or West. Thus direction of flight seems to be the most important variable in the degradation of performance on June 17, in this region.

Table 1. Estimations of race performances of 30 clubs on June 17, 1972, as better than (B), the same as (S), or worse than (W) the same clubs' performances previously (see text for explanation of ratings). Breakdown according to direction of race: octants N/S = north or south  $\pm 22.5^\circ$ ; Diag = NE, NW, SW, SE  $\pm 22.5^\circ$ ; E/W = east or west  $\pm 22.5^\circ$ . Judges: CCB, Beegle; PHC, Carr; WPS, Switzer.

Judge	N/S			Diag			E/W		
	B	S	W	B	S	W	B	S	W
CCB	3	4	0	0	6	5	3	2	7
PHC	2	5	0	0	5	6	1	4	7
WPS	2	5	0	0	5	4	0	6	8
Totals	7	14	0	0	16	15	4	12	21

Table 2. Estimations of race performances of 30 clubs on June 17, 1972, as better than (B), the same as (S), or worse than (W) the same clubs' performances previously. Breakdown according to region of location of home (see text for explanation of ratings). Judges: CCB, Beegle; PHC, Carr; WPS, Switzer.

Judge	West			Central			East		
	B	S	W	B	S	W	B	S	W
CCB	4	3	0	1	5	3	1	4	9
PHC	2	5	0	1	5	3	0	4	10
WPS	1	6	0	1	7	1	0	3	11
Totals	7	14	0	3	17	7	1	11	30

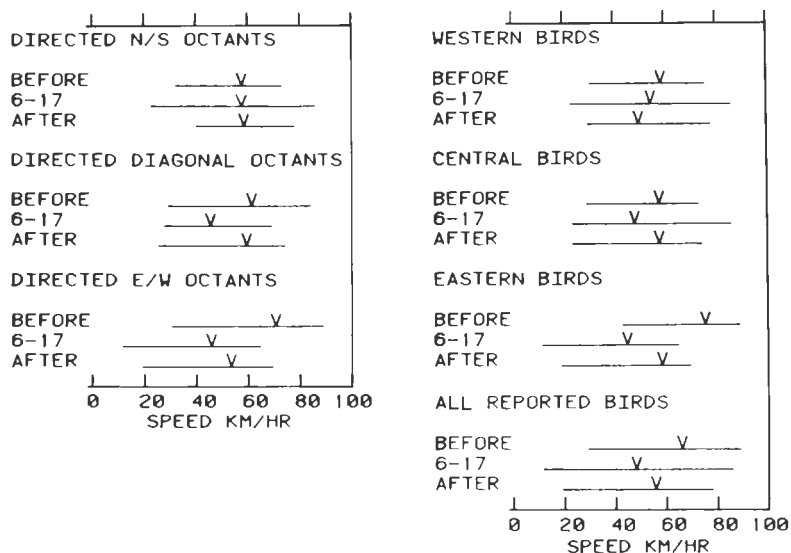


Figure 3. Speed data for reporting racing pigeons in races before, on, and after June 17, 1972, categorized according to direction and location of the races. Horizontal lines indicate range of speed; the superimposed V the average speed. Octants N/S = north or south  $\pm 22.5^\circ$ ; diagonal = NE, NW, SW, SE  $\pm 22.5^\circ$ ; E/W = east or west  $\pm 22.5^\circ$ . Western, Central, Eastern refer to home regions (see also Tables 3 and 4).

We were not entirely satisfied with the analysis resting so heavily on subjective judgments, and therefore we tried to gain more objective quantitative evaluations from the available data in the *Racing Pigeon Bulletin*. The only measured quantities given in the reports were number of birds in the race, number of birds whose performance is reported, speed of each reported bird in yds/min, and length of the race in miles. (We have converted speeds to km/hr and miles to km. For pigeon racers who might read this article, the conversion factors are as follows: km/hr to yds/min, multiply by 18.23; km to miles, multiply by 0.621.) For the moment we ignore the length of the race and attend only to the speed as a measure of performance; length of race will be considered later.

As described above, we compared the data for the races of June 17 with those for the two (combined) races before that date and for the race following it. The overall results of this analysis are displayed in Figure 3 and Tables 3 and 4. Ranges of speeds are shown in the figure, while the numbers of reported birds are given in the tables. Statistical treatment is complicated by the inconsistencies in the base populations; analysis of variance by unweighted means, however, provides some confidence in the following interpretations. In regard to *direction* of the races, the speed data agree well with the

Table 3. Comparison of average speeds (km/hr) of reported birds in 31 races on June 17, 1972, with races before and after that date (see also Fig. 3). Breakdown according to direction of race: octants N/S = north or south  $\pm 22.5^\circ$ ; Diag = NE, NW, SW, SE  $\pm 22.5^\circ$ ; E/W = east or west  $\pm 22.5^\circ$ . The figures in parentheses are the number of birds reported.

	N/S	Diag	E/W	Ave. Total
Before	57.6 (112)	61.4 (157)	70.7 (415)	63.2 (684)
June 17	57.3 (73)	45.3 (78)	45.8 (194)	49.4 (345)
After	58.7 (32)	59.4 (54)	53.3 (111)	57.1 (197)

Table 4. Comparison of average speeds (km/hr) of reported birds in 31 races on June 17, 1972, with races before and after that date (see also Fig. 3). Breakdown according to region of location of home: W = west; C = central; E = east. The figures in parentheses are the numbers of birds reported.

	W	C	E	Ave. Total
Before	58.7 (150)	57.8 (210)	75.5 (324)	64.0 (684)
June 17	54.7 (83)	47.9 (105)	44.8 (157)	49.0 (345)
After	49.8 (52)	57.7 (93)	58.6 (52)	55.3 (197)

conclusions of the judges on performance: a degradation is most definite on June 17 for E/W and to a lesser degree for diagonal octants, and none for N/S. In regard to *location* of the races, again there is agreement with the judges' conclusions: the West region exhibited no indication of effect of the magnetic disturbance, while the East region showed considerable degradation and the Central region was intermediate, only the Chicago races being "smashes."

Overall, the race data may suggest some additional thoughts. For the two races (combined) before June 17, of 18,805 birds flown, 684 were reported (3.6%) with average speed about 64 km/hr. In the June 17 races 7,857 birds were flown, of which 345 were reported (4.4%) with average speed about 49 km/hr. In the race following June 17, of 3,631 birds flown, 197 were reported (5.4%) with average speed about 56 km/hr. The reduced number of birds flown in the latter race may indicate a loss of birds June 17, but such is not reported in the *Racing Pigeon Bulletin*. If the best racing birds rely on the Earth's magnetic field as a navigational aid, they probably would be the ones most likely to be lost in times of severe magnetic disturbance. Perhaps this is the reason for the somewhat reduced average speeds in the race after June 17.

Two other variables can also be evaluated from the race data: length of race and familiarity of the birds with the particular course. Assuming that speeds are a linear function of length of race (an exponential function was found to give a poorer fit), we took the data of the two races preceding June 17 and calculated the linear relation, and then extrapolated or interpolated for the length of the June 17 race to obtain a projected average speed. This procedure was possible for 25 of the 31 clubs. Performance of a club is measured as the percentage increase of the actual June 17 average speed divided by the projected:  $\text{performance} = 100(\text{actual} - \text{projected})/\text{projected}$ . Table 5 presents the results categorized according to race direction and region. Again the conclusions of the judges that the East region and the E/W directed races had worse performance than expected were supported; only the slightly better than projected performance of the Central clubs was contrary.

Regarding the question of familiarity of the birds with the course of the June 17 races, we shall assume that experience should improve performance. From information about the two preceding races, four categories of familiarity were set up. The relations of these categories to club region and to race direction are presented in Tables 6 and 7, respectively. There seems to be no bias of experience in the three regions, but the birds flying N/S on June 17 were much more familiar with the routes than those flying E/W. The fact that most of the East region races were E/W again confounds the issue.

## DISCUSSION

At the beginning of our study we were aware of Yeagley's (1947) pioneering though controversial experiments with a magnetic hypothesis. Meanwhile Keeton and others were resuscitating the idea of a magnetic sense as a physical guide in bird navigation, and in recent years it has gained general acceptance. Still, the demonstration of such sensitivity and its possible mechanism has been difficult and elusive (Bookman, 1978; Keeton et al., 1974; Kiepenheuer, 1978; Larkin and Keeton, 1976; Visalberghi and Alleva, 1979;

Table 5. Performance of clubs, race of June 17, 1972, as measured by the percentage increase of the actual speed over the projected speed (see text for calculation). The numbers in parentheses are the number of clubs.

Race Directed Octants	Home Region Group			Ave. Totals
	West	Central	East	
N/S	27.6 (2)	24.9 (4)	0 (0)	25.8 (6)
Diag.	-3.2 (1)	14.6 (2)	-40.8 (3)	-16.1 (6)
E/W	15.0 (3)	-73.6 (1)	-29.9 (9)	-22.9 (13)
Totals	16.2 (6)	7.9 (7)	-32.6 (12)	-9.5 (25)

Table 6. Familiarity of birds with the course of the race flown June 17, 1972, measured by the number of clubs. Categories: A = June 17 course exactly same as at least one previous; B = June 17 course an extension of at least one previous; C = June 17 course a portion of at least one previous; D = June 17 course unrelated to any previous. The numbers in parentheses are percentages of the number of clubs in a region (West, Central, or East), except for the totals where they are percentages of the total number of clubs.

Category	Club Home Region			Totals
	West	Central	East	
A	2 (25.0)	3 (33.3)	4 (28.6)	9 (29.0)
B	4 (50.0)	3 (33.3)	5 (35.7)	12 (38.7)
C	1 (12.5)	2 (22.2)	3 (21.4)	6 (19.4)
D	1 (12.5)	1 (11.1)	2 (14.3)	4 (12.9)
Totals	8 (25.8)	9 (29.0)	14 (45.2)	31 (100.0)



Table 7. Familiarity of birds with the course of the race flown June 17, 1972, measured by the number of clubs. Categories: same as in Table 6. The numbers in parentheses are percentages of the number of clubs racing June 17 in the directed octant groups, except for the totals where they are percentages of the total number of clubs.

Category	Directed Octants June 17			Totals
	N/S	Diag	E/W	
A	3 (42.9)	3 (27.3)	3 (23.1)	9 (29.0)
B	0 (0)	4 (36.4)	8 (61.5)	12 (38.7)
C	3 (42.9)	3 (27.3)	0 (0)	6 (19.4)
D	1 (14.2)	1 (9.1)	2 (15.4)	4 (12.9)
Totals	7 (22.6)	11 (35.5)	13 (41.9)	31 (100.0)

Walcott, 1977, 1978; Wallraff, 1978; Wiltshko, et al., 1978, 1981). Keeton (1974a, 1974b) has excellently reviewed the history and complexities of studies of navigation by homing pigeons, and the 1977 Symposium on Animal Migration, Navigation, and Homing gave a very broad view of recent research. A more recent review of the problems of magnetic sensitivity is provided by Gould (1980). The discovery of "biogenic magnetite" in the heads of pigeons and other animals (Kirschvink and Gould, 1981; Presti and Pettigrew, 1980; Walcott et al., 1978; and Zoeger et al., 1981) is an exciting advance.

Our study differs from most others in that we were concerned with the performance of flocks. Other investigators have generally preferred to make observations on individual-bird releases, especially regarding initial orientation (bearing at departure), in part for statistical rigor. Scientists in general, however, have not been involved in the sport of pigeon racing, and the racing data have been given little attention. Yeagley (1951), it is true, did include race results in his considerations and noted a negative relation between performance and an index of increasing sunspot activity. Also, Schreiber and Rossi (1976) utilized race results in a similar study, with similar conclusions. Their data were derived from 18 successive races from 1932-1957, Belvedere to Parma (Italy; about 730 km = 450 mi). Sunspot activity index for each date and percentage arrivals the same day showed a strong negative relation. More research of this sort seems possible and highly desirable.

Although the AME club members were probably convinced that magnetic storms should be avoided if possible in future races, others may reserve judgment. After all, we found no degradation with N/S races, and none in the Western region of the United States from the June 17, 1972, disturbance. Also, so far as we could learn, the only "smashes" on June 17 were the two races from Nebraska to Chicago. What mitigation is there for such inconsistencies?

We think there is no good reason to expect a magnetic storm to upset N/S navigation. The streams of charged particles from a solar flare are directed by the Earth's magnetic field into orbits about the magnetic axis and produce a magnetic field of their own which adds to that of the Earth. The result is rapid changes in all three components (the vertical and two horizontal) of the field at the Earth's surface. Magnetic storms, as these disturbances are called, when rather severe may produce fluctuations as large as one percent. The storm of June 17, 1972, gave changes in the field intensity (the vector sum of the three components) of about 400 gammas, where the normal intensity in the region of the races is about 55,000 gammas (100,000 gammas = 1 gauss). Because the magnetic north pole is deep under the northern tip of Greenland, the vertical component is the major one; the changes in the horizontal components would not have changed the indication of man's magnetic compass by as much as one degree. This deviation is not serious from a navigational standpoint. Therefore, we may conclude that if the pigeon has a magnetic sense it is not of the kind that indicates direction in the horizontal plane, but rather responds to differences in intensity (Kirschvink and Gould, 1981).

The intensity or strength of the Earth's field increases from a minimum at the magnetic equator to a maximum at the pole. In the northern midwestern United States, the undisturbed intensity increases roughly 2.7 gammas/km (4.4 gammas/mile) of latitude. Thus, the pigeon could interpret changes in intensity as displacement north or south. To take an example, suppose the bird is released some distance west of home; in undisturbed conditions he would sense no change of latitude, and other cues should direct him eastward. But if a magnetic storm is in progress, with changes in intensity of as high as 180 gammas/hr, as in the June 17 storm, he would feel that he had drifted north (increased intensity) or south (decreased intensity) by many miles and would attempt to compensate. This is exactly the situation during part of the afternoon-evening of June 17 in the Nebraska-Chicago races. The magnetogram (Fig. 1) actually is a considerably smoothed curve, as the actual fluctuations may be several per second and though strong not show up on the graph. Unsteadiness began about 8 a.m. (CDT). By 4 p.m. the birds were in a very confusing magnetic field which continued past the time the birds would have to stop for darkness, and they might not have made much progress eastward.

According to such reasoning, let us say that the pigeon is flying in calm air at 50 km/hr, and during one half hour the field intensity increased 90 gammas. To overcome the feeling of drift, the bird should fly southward from east. In fact, he soon finds that he has to head straight south. As he flies south at 50 km/hr he is flying into weaker intensity at the rate of  $50 \times 2.7 = 135$  gammas/hr, but the storm is strengthening the field at the rate of 180 gammas/hr, so that he thinks he is still drifting north. At the end of this half hour, he thinks he is 22.5 gammas (8.3 km) north of the start when in fact he is 25 km south. Now the storm begins decreasing the intensity at the same

rate, 180 gammas/hr. The bird continues heading south, and his sensor indicates falling intensity at the rate of  $50 \times 2.7 + 180 = 315$  gammas/hr. In about 4.3 minutes he would feel that he has returned to the original latitude, by which time he has actually progressed further south to a point about 28.6 km south of the original course line. When he then heads east he finds this is not right because the intensity is still decreasing 180 gammas/hr. To compensate he heads north, but he cannot win—at his best the intensity is still decreasing at 45 gammas/hr. At the end of the hour he feels he is still about 19.3 gammas (7 km) south of the original course. Actually he is right—he has made back to the north 21.4 km of the 28.6 km he was south at the worst. He now knows where he is. However, when he turns east it so happens in the June 17 case that the intensity has started to increase rapidly, and the cycle starts all over. As long as the rate of change of intensity is more rapid than the bird can change the field by his flight speed along the gradient of the field, the bird would tend to fly north and south alternately, and only slowly to the east. Presumably the birds would not only be confused but also tired.

This interpretation says that the time derivative and period of the plot of magnetic intensity versus time is more important than the actual values of magnetic intensity itself for confusing pigeons desiring to fly east or west. In the above example, the critical rate of change of magnetic intensity is 135 gammas/hr. During many portions of the storm, the rate of change is not so rapid. If the increase is 60 gammas/hr, as it was for two hours early in the June 17 storm, and if the bird is clever, he would direct his flight 26.4 degrees south of east. He would thus advance eastward at  $50 \times \cos 26.4^\circ = 44.8$  km/hr, while at the same time losing magnetic intensity by flight at  $50 \times \sin 26.4^\circ = 60$  gammas/hr, the same rate the storm is increasing intensity. He would feel satisfied, but at the end of two hours he would be  $2 \times 50 \times \sin 26.4^\circ = 44.5$  km south of the desired course, and only 90 km east of the starting point. Later the storm will decrease the magnetic intensity, and the bird would angle back toward the desired course, but at home longitude it would be pure chance how far north or south he would be. He might then fly north and south alternately (depending on the storm) until close enough to home to recognize landmarks visually.

For a bird with a north destination, the situation is much different. Again assuming calm air and the bird's speed at 50 km/hr, with a field intensity increase of 90 gammas in the first half hour, we calculate the bird should feel that he has made great progress. The storm and his motion cooperate to make him feel that he is increasing the intensity at 315 gammas/hr for the half hour, a gain of  $315/2 = 157.5$  gammas toward his goal. In the next half hour, if we assume the same rate of decreasing intensity, he quickly discovers he is losing ground, but the least loss occurs if he keeps the north heading. Now he feels he is slipping backward at 45 gammas/hr, or 22.5 gammas = 8.33 km for that half hour. Hence the feeling at the end of the hour is a gain of  $58.33 - 8.33 = 50$  km in the direction he wanted to go. Actually he has been moving over the ground all the time at 50 km/hr northward, so that he is right. He knows where he is and has lost no time. Presumably as he approaches home he will recognize the territory and home visually, though perhaps a sharp decrease in field intensity might cause temporary overshooting. We would therefore not expect the magnetic storm to have significant degradation effect on the race performance, for N/S direction.

The lack of degradation of performance of the birds in E/W races in the western region of the country now needs attention. As indicated earlier, those birds had more familiarity with the course than the birds in other regions had, and thus might have been able to ignore the storm. Also, about half of their course followed the Snake River, and there may be a strong tendency to follow valleys. In such areas perhaps the magnetic sense is subordinate. But there is still another possible explanation: training of the birds in the west is during generally more favorable climatic conditions than in the east, and the birds may come to depend more on vision in the west.

One may also wonder whether some peculiar feature of those E/W races favored the western region. All of the races in that category there (total = 3) were directed westward, while all of the central and eastern E/W races were directed eastward. According to our argument above, no difference in response would be expected.

Finally, could the birds participating in the three western races in question have reached home before the magnetic storm became intense? These were approximately 400-mile races and would probably have taken at least eight hours (at 80 km/hr) for the fastest birds to home. But during this period the magnetic storm was becoming intense and should have confused most of the birds.

The birds involved in this study were mostly reared and trained during a time of "quiet" sun: sunspots were few, and consequently solar flares were infrequent and magnetic storms were very rare. We might reason that the birds had come to trust the Earth's magnetic field, but on June 17, 1972, they were let down. Would pigeons reared and trained during the time of "active" sun have the same problem of navigation E/W when there is a magnetic storm, or could they ignore it? We think this (among related questions) is a topic that should be investigated in the future. The years 1980-1981 were a period of "active" sun, and some racers have noted severe training losses in 1981. They are not inclined to publicize "smashes."

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## A REEVALUATION OF MATHEMATICAL MODELS FOR PREDICTING VARIOUS PROPERTIES OF LOESS-DERIVED SOILS IN IOWA<sup>1</sup>

T. L. Coleman and T. E. Fenton<sup>2</sup>

**ABSTRACT.** This study reevaluates equations for predicting various properties of loess-derived soils in the loess province of Iowa. Measurements of the thickness of the loess, maximum clay content in the B horizon, B/A clay ratio, drainage class, and the distance from the loess source area were made on twenty-one sites on primary upland divides.

Loess thickness decreased systematically with distance from the loess source area. Maximum clay content in the B horizon and the B/A clay ratio increased with distance from the source area as the internal drainage of the major soils became poorer and as loess thickness decreased. The previously proposed equations for predicting loess thickness and the equations proposed in this paper all are adequate for predicting the thickness of the loess in the southwestern loess province of Iowa. The previously proposed equations for predicting maximum clay content in the B horizon and B/A clay ratio were found inadequate for describing the data obtained in this study.

The multi-variable equations proposed in this paper for predicting the maximum clay content in the B horizon and B/A clay ratio of the loess-derived soils provided a better fit of the data than did the single-variable equations of previous authors as indicated by higher coefficients of determination. However, due to the effects of intercorrelation, the variability in the dependent variables attributable to the combined effect of the independent variables of the equations was small.

Additional index words: Loess thickness, Maximum clay content, B/A ratio, Soil drainage class, Water tables.

## INTRODUCTION

Loess deposits cover a large portion of the midcontinent of the United States. The area of their occurrence extends from the Great Plains on the west to the Ohio River Basin on the east and south to the Gulf of Mexico. Loess-derived soils within these areas form a repetitive pattern on the landscape. Their systematic occurrence makes it possible to formulate mathematical models for predicting certain properties of these soils.

Prediction equations have been proposed by Hutton (1947), Ulrich (1950), Ulrich and Riecken (1950), Ruhe (1969), and Worcester (1973) for the loess province of Iowa. Krumbein (1937), Smith (1942), and Frazee et al. (1970) formulated equations for loess deposited in Illinois. However, they used

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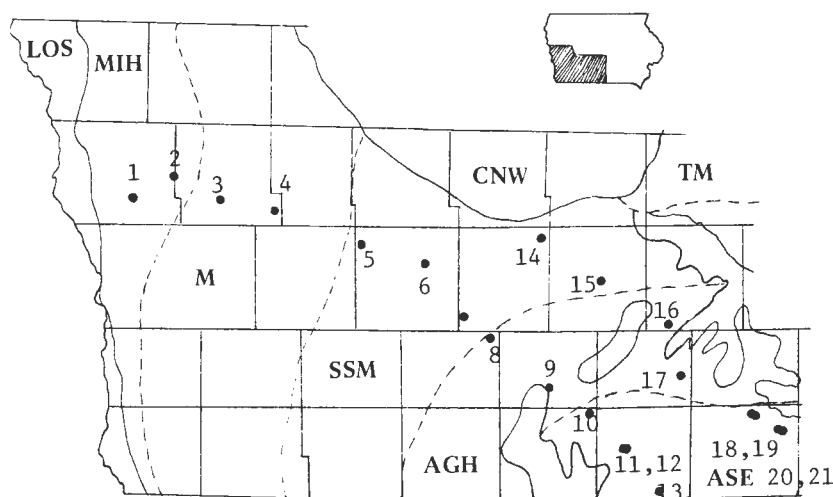


Figure 1. Sketch of southwestern Iowa showing site locations and the major soil associations. LOS is Luton-Onawa-Salix, MIH is Monona-Ida-Hamburg, M is Marshall, SSM is Shelby-Sharpsburg-Macksburg, AGH is Adair-Grundy-Haig, ASE is Adair-Seymour-Edina, CNW is Clarion-Nicollet-Webster, and TM is Tama-Muscatine soil association areas. Numbers indicate locations of sampling sites.

only a single variable, which was either thickness of the loess or distance from the major source area.

Many properties of loess-derived soils are directly affected by the moisture status of the soils, the quantity of water that moves through the profile, and that which remains in the solum. The maximum clay content in the B horizon and the B/A clay ratios (maximum clay content in the B horizon/minimum clay content in the A horizon) are two such soil properties. The best indication of the moisture status of these soils is their moisture regime as reflected by the depth to the water table and its duration. The presence of a water table in the solum of some soils in this area has been reported by Ruhe (1969) and Worcester (1973), and a complete review has been presented by Coleman (1980). In the present study, multiple variables are utilized in formulating prediction equations to obtain a more accurate prediction of these soil properties.

## METHODS AND MATERIALS

The loess province of southwestern Iowa was chosen as the location of this study (Figure 1). Twenty-one sites on stable (2% slope) primary upland divides were selected in the five major soil association areas that represent a

continuum of increasing degree of horizon differentiation in the loess-derived soils. These are (Oschwald et al., 1965): Monona-Ida-Hamburg (MIH), Marshall (M), Shelby-Sharpsburg-Macksburg (SSM), Adair-Grundy-Haig (AGH), and Adair-Seymour-Edina (ASE). Classification of the soils at the subgroup level and their natural drainage class are listed in Table 1.

Loess thickness measurements were made by using a Giddings hydraulic soil coring machine. The thickness of the loess was measured from the ground surface to the contact between the loess and underlying non-loess materials.

The natural drainage class of each soil pedon was determined based on the criteria outlined in the Soil Survey Manual (Soil Survey Staff, 1951). The drainage classes were coded into numerical values for later use in regression analyses. The coded values used were 10, 20, 30, and 40 for well, moderately well, somewhat poorly, and poorly drained soils, respectively. The depth to deoxidized loess was determined by the criteria of Hallberg et al. (1978).

Particle size distribution was determined by the pipette method (Kilmer and Alexander, 1949) as modified by Walter et al. (1978). The B/A clay ratio was determined by dividing the maximum amount of clay in the B horizon by the minimum amount of clay in the A horizon.

## RESULTS AND DISCUSSION

### Loess Thickness Relationships and Trends

Loess thickness decreased as distance from the major loess source area (Missouri River Valley) increased. This relationship may be described mathematically by Equation 1:

$$Y = 2886.39 - 482.261nX \quad (1)$$

where Y is loess thickness in cm and X is distance from the loess source in km (Figure 2). The coefficient of determination value which represents the effect distance from the loess source has on loess thickness is 0.959.

Mathematical models expressing the relationships between loess thickness and distance from the source area have been proposed by Hutton (1947) and Worcester (1973) for loess deposits in Iowa. Data from the present study used in fitting regressing equations of these authors provided coefficients of determination of 0.900 and 0.899, respectively (Table 2). The data used in formulating Hutton and Worcester's equation were used in fitting Equation 1. The resulting coefficients of determination are 0.912 and 0.970, respectively (Table 2). These coefficients of determination show that Equation 1 is more effective in comparison to the previously proposed equations in explaining the effect distance from the loess source has on loess thickness.

### Maximum Clay Relationships and Trends

The maximum clay content in the B horizon of the soils studied increased in the B horizon of the soils as the thickness of the loess decreased and with increasing distance from the loess source. This relationship may be described mathematically by Equation 2:

$$Y = 108.45 - 11.20 \ln X \quad (2)$$



Table 1. Soil type, classification, and natural drainage class at each study site.

Site	Soil Type	Classification	Natural drainage class
1	Monona sil	Typic Hapludoll	well
2	Monona sil	Typic Hapludoll	well
3	Marshall sil	Typic Hapludoll	well
4	Minden sil	Aquic Hapludoll	somewhat poorly
5	Sharpsburg sicl	Typic Argiudoll	mod well
6	Macksburg sicl	Aquic Argiudoll	somewhat poorly
7	Sharpsburg sicl	Typic Argiudoll	mod well
8	Winterset (var) sil	Typic Argiaquoll	poorly
9	Haig sicl	Typic Argiaquoll	poorly
10	Haig (var) sicl	Typic Argiaquoll	poorly
11	Edina sicl	Typic Argialboll	poorly
12	Haig sil	Typic Argiaquoll	poorly
13	Edina sil	Typic Argialboll	poorly
14	Macksburg sicl	Aquic Argiudoll	somewhat poorly
15	Ladoga sicl	Mollic Hapludalf	mod well
16	Haig sicl	Typic Argiaquoll	poorly
17	Haig sil	Typic Argiaquoll	poorly
18	Edina sil	Typic Argialboll	poorly
19	Pershing sicl	Udolic Orchraqualf	somewhat poorly
20	Edina (var) sicl	Typic Argialboll	poorly
21	Edina sil	Typic Argialboll	poorly

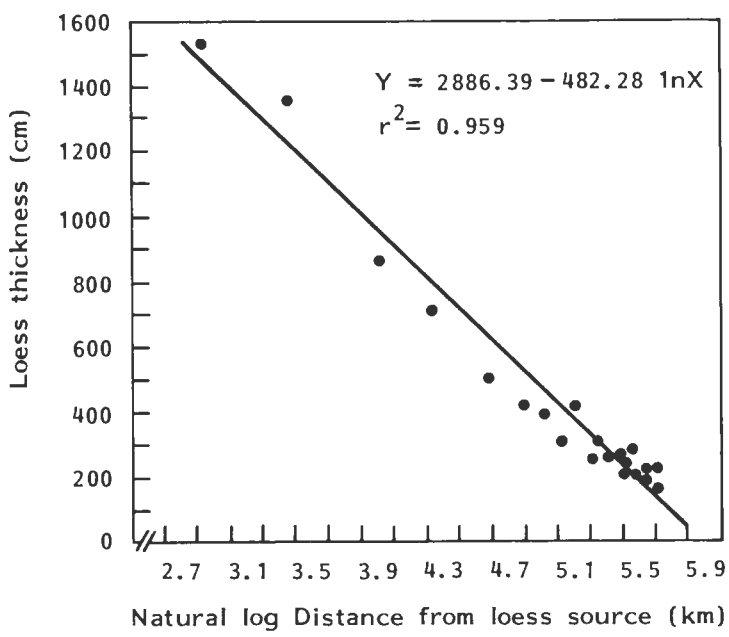


Figure 2. Relationship between loess thickness and the natural log of distance from loess source.

where Y is the maximum clay content in the B horizon and X is loess thickness in cm (Figure 3). The coefficient of determination value is 0.852.

The relationship between maximum clay content in the B horizon and distance from the loess source may be described mathematically by Equation 3:

$$Y = 27.88 + 0.08X \tag{3}$$

where Y is the maximum clay content in the B horizon in percent and X is the distance from the loess source in km (Figure 4). The coefficient of determination value is 0.832.

Data in Table 3 show that a positive relationship exists between maximum clay content in the B horizon and the natural drainage class (DRA). The variables have a correlation coefficient of 0.898. This indicates that as the soils become poorly drained, the maximum clay content in the B horizon of the loess-derived soils increases.

The relationship between maximum clay content, loess thickness, and DRA may be described mathematically using Equation 4:

$$Y = 2.74 + 0.06X_1 + 15.20 \ln X_2 - 0.03X_1 \ln X_2 \tag{4}$$

where Y is the maximum clay content in the B horizon in percent, X1 is loess thickness in cm, and X2 is the natural drainage class code. The coefficient of

Table 2. Coefficient of determination values computed from equations predicting loess thickness, maximum clay content of the B horizon, and B/A clay ratios.

Author of Equation	Equation	Variables <sup>a</sup>		Coefficient of Determination	Source of Data
		Dep.	Indep.		
Coleman	Eq.-1	L.T	Dist.	0.959	Coleman, 1980
Hutton		L.T	Dist.	0.900	Coleman, 1980
Worcester		L.T	Dist.	0.899	Coleman, 1980
Coleman	Eq.-1	L.T	Dist.	0.912	Hutton, 1947
Coleman		L.T	Dist.	0.970	Worcester, 1973
Coleman	Eq.-2	Max. Clay	L.T	0.852	Coleman, 1980
Ulrich		Max. Clay	L.T	0.237	Coleman, 1980
Coleman	Eq.-2	Max. Clay	L.T	0.876	Worcester, 1973
Coleman	Eq.-3	Max. Clay	Dist.	0.832	Coleman, 1980
Ulrich		Max. Clay	Dist.	0.144	Coleman, 1980
Worcester		Max. Clay	Dist.	0.001	Coleman, 1980
Coleman	Eq.-3	Max. Clay	Dist.	0.911	Worcester, 1973
Coleman	Eq.-3	Max. Clay	Dist.	0.733	Ulrich, 1950
Coleman	Eq.-3	Max. Clay	Dist.	0.775	Hutton, 1947
Coleman	Eq.-3	Max. Clay	L.T + DRA	0.902	Coleman, 1980
Coleman	Eq.-3	Max. Clay	L.T + DRA	0.899	Worcester, 1973
Coleman	Eq.-4	B/A ratio	L.T	0.546	Coleman, 1980
Coleman	Eq.-5	B/A ratio	Dist.	0.656	Coleman, 1980
Coleman	Eq.-6	B/A ratio	L.T + DRA	0.677	Coleman, 1980
Ulrich		B/A ratio	Dist.	0.435	Coleman, 1980
Worcester		B/A ratio	L.T	0.082	Coleman, 1980
Coleman	Eq.-5	B/A ratio	L.T	0.473	Worcester, 1973
Coleman	Eq.-5	B/A ratio	Dist.	0.640	Worcester, 1973
Coleman	Eq.-6	B/A ratio	L.T + DRA	0.667	Worcester, 1973

<sup>a</sup>L.T is a loess thickness; Max Clay is maximum clay content of B horizon; Dist. is distance from source; DRA is natural drainage class code.

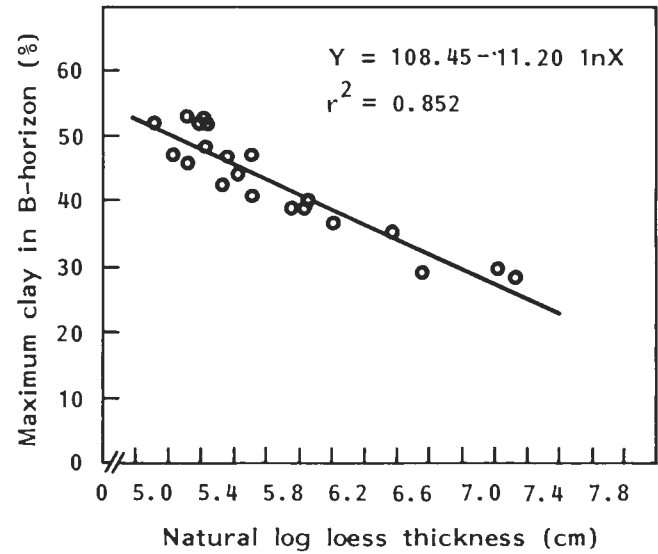


Figure 3. Relationship between maximum clay content of the B horizon and the natural log of loess thickness.

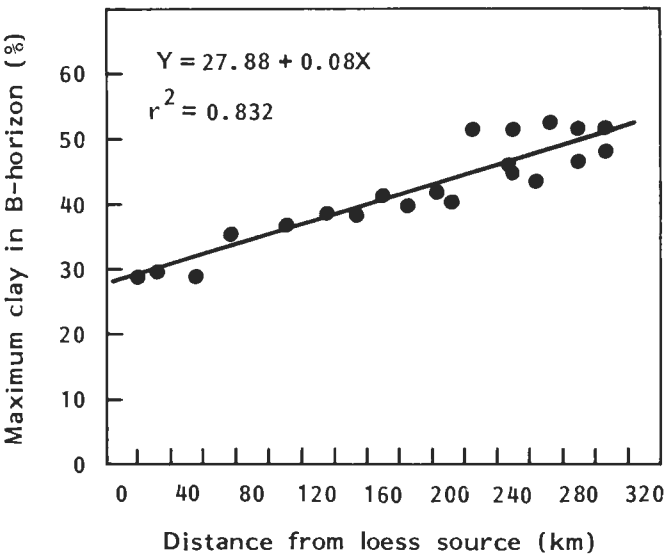


Figure 4. Relationship between maximum clay content of the B horizon and distance from loess source.

Table 3. Correlation matrix of selected variables.

Variables <sup>a</sup>	LT-cm	Dist-km	Max-Clay	AVC-AP	B/A	DRA	DTDL-cm
LT-cm	1.000						
Dist-km	-0.870**	1.000					
Max-Clay	-0.841**	0.912**	1.000				
AVC-AP	0.181	-0.485*	-0.478*	1.000			
B/A	-0.635**	0.810**	0.850**	-0.787**	1.000		
DRA	-0.815**	0.865**	0.898**	0.372 <sup>++</sup>	0.754**	1.000	
DTDL-cm	0.932**	-0.677**	-0.668**	0.029	-0.459**	-0.637**	1.000

<sup>a</sup>LT-cm = loess thickness in cm; Dist-km = distance from loess source in km; Max-Clay = maximum clay in the B horizon in percent; AVC-AP = average clay content of the plow layer; B/A = ratio between the maximum clay in B horizon versus the minimum clay content in the A horizon; DRA = drainage class; DTDL-cm = depth to deoxidized loess in cm.

\*\*, \*, and <sup>++</sup> denote significance at the 1, 5, and 10 percent levels, respectively.

determination, 0.902, represents the combined effect of these variables on the maximum clay content in the B horizon. This is an increase of 5 and 7 percent over Equations 2 and 3, respectively. The small increase in the coefficient of determination using Equation 3 may be attributed to intercorrelation existing between the independent variables. Data in Table 3 show that significant correlation exists between DRA and loess thickness, loess thickness and maximum clay content in the B horizon, and DRA and maximum clay content in the B horizon (-0.815, -0.841, and 0.898, respectively). These values infer that the variables, when used in the same equation to explain sources of variation in the dependent variable (maximum clay), may be accounting for the same variation, which will have a tendency to suppress the effectiveness of each variable. In light of this, the simpler equations should be used.

The relationship between maximum clay, distance from the loess source, and loess thickness has been described mathematically by Ulrich (1950) and Worcester (1973). Coefficients of determination produced using their equations and the data from the present study (Table 2) show that these equations poorly fit the data. However, the Ulrich and Worcester data were fitted to Equations 2 and 3; an adequate fit was obtained as indicated by higher coefficients of determination (Table 2).

B/A Clay Ratio Relationships and Trends

The B/A clay ratio of the soils studied showed an increase in the B/A clay ratio as the thickness of the loess decreases and with increasing distance from the loess source. These relationships can be expressed mathematically by Equation 5:

$$Y = 5.34 - 0.62 \ln X \tag{5}$$

where Y is the B/A clay ratio and X is loess thickness in cm (Figure 5) and Equation 6:

$$Y = 0.78 + 0.005X \tag{6}$$

where Y is the B/A clay ratio and X is distance from the loess source in km (Figure 6). The coefficients of determination are 0.546 and 0.656, respectively.

Data in Table 4 show that a positive relationship exists between B/A clay ratio and DRA. The variables have a correlation coefficient of 0.754, which indicates that as the soils become more poorly drained the B/A clay ratio increases. The relationship between B/A clay ratio, loess thickness, and DRA may be described mathematically using Equation 7:

$$Y = 1.60 + 0.006 X_1 + 1.22 \ln X_2 - 0.003 X_1 \ln X_2 \tag{7}$$

where Y is the B/A clay ratio, X<sub>1</sub> is loess thickness in cm, and X<sub>2</sub> is the natural drainage class code. The coefficient of determination is 0.677. This is an increase of 3.1 and 2.1 percent over Equations 5 and 6, respectively. This small increase may be attributed to the effect of intercorrelation as explained in the preceding paragraphs discussing maximum clay content.

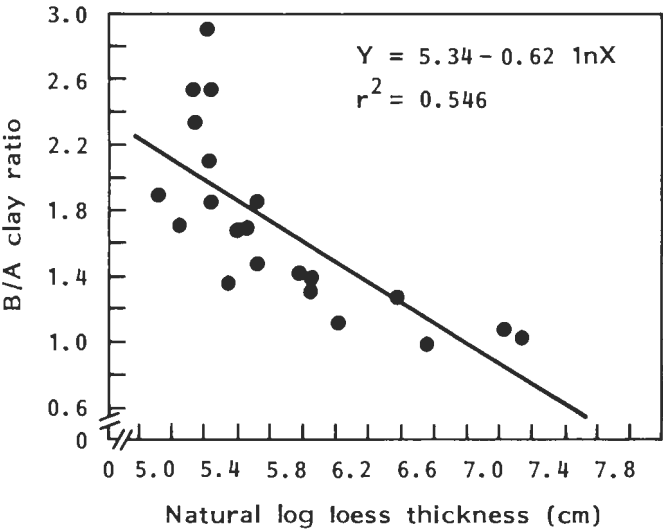


Figure 5. Relationship between B/A clay ratio and the natural log of loess thickness.

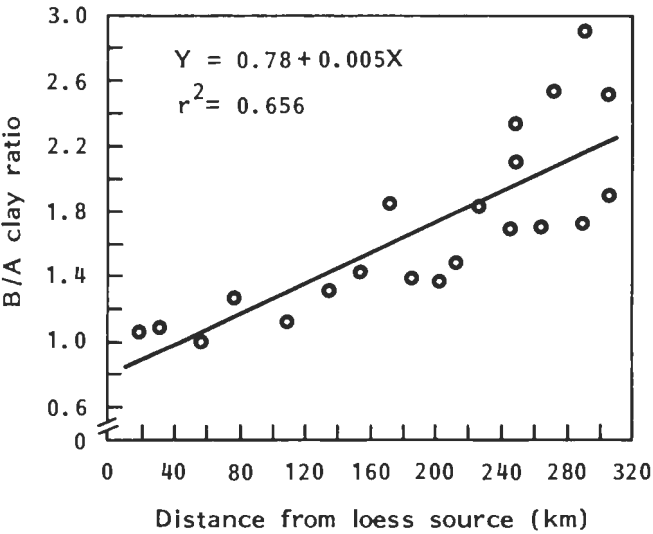



Figure 6. Relationship between B/A clay ratio and distance from loess source.

Table 4. Flow chart of the relative degree of horizon differentiation of the loess-derived soils of this study.

Site	Classification	Max-Clay <sup>a</sup>	B/A Ratio <sup>b</sup>	DRA <sup>c</sup>	Stage of Development
1, 2, 3	Typic Hapludolls	29.3	1.05	10	Minimal
4	Aquic Hapludolls	35.5	1.27	20	
5, 7	Typic Argiudolls	37.6	1.27	20	
6, 14	Aquic Argiudolls	39.2	1.36	30	
8, 9, 10, 12, 16, 17	Typic Argiaquolls	47.1	1.76	40	
11, 13, 18, 20, 21	Typic Argialbolls	50.0	2.44	40	Maximal

<sup>a</sup>Average maximum clay in solum of soils.

<sup>b</sup>Average B/A clay ratio of soils.

<sup>c</sup>Average natural drainage class code of soils.

The relationship between B/A clay ratio, distance from the loess source, and loess thickness has been described mathematically by Ulrich (1950) and Worcester (1973). Application of the data from this study to their equations (Table 2) produces lower coefficients of determination and, therefore, explains less of the variability in B/A clay ratio as compared to Equations 5 and 6. However, when the data used to formulate Worcester's equation are fitted to Equations 5, 6, and 7, the coefficient of determination values resulting are close to those produced using the data from our work. This indicates that Equations 5, 6, and 7 are more adequate in predicting the B/A clay ratio of the loess-derived soils than those previously proposed by Ulrich (1950) and Worcester (1973).

#### Relationship to Horizon Differentiation

Loess thickness and the physical properties of the loess-derived soils studied also are related to the relative degree of horizon differentiation (Table 4) as reflected in the maximum clay content in the B horizon, B/A clay ratio, and natural drainage class. Horizon differentiation increased as the maximum clay content in the B horizon and B/A clay ratio increased and as the internal drainage of the soils became poorer.



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## HERBAGE CATION CONCENTRATIONS IN SWITCHGRASS, BIG BLUE-STEM, AND INDIANGRASS WITH NITROGEN FERTILIZATION<sup>1</sup>

J. R. George and K. E. Hall<sup>2</sup>

**ABSTRACT.** Cation concentrations in native, perennial, warm-season grass herbage have not been thoroughly evaluated when grown in a humid region. This study was conducted to measure potassium (K), calcium (Ca), and magnesium (Mg) concentrations in herbage of switchgrass (*Panicum virgatum* L.), big bluestem (*Andropogon gerardi* Vitman), and Indiangrass (*Sorghastrum nutans* L. Nash). Nitrogen (N) was applied at 0, 75, and 150 kg-ha<sup>-1</sup> as urea (45-0-0) on 22 May and again on 3 July after the first harvest. Plots were harvested on 30 June and again on 2 September at a 20-cm cutting height. Mean herbage K (0.92 to 0.99%) and Ca (0.46 to 0.47%) concentrations were similar among grass species, but Mg was variable: switchgrass, 0.43%; big bluestem, 0.33%; and Indiangrass, 0.22%. Nitrogen fertilization decreased herbage K concentration for the 2 September but not for the 30 June harvest date. Herbage Ca and Mg generally showed a linear increase with N fertilization. Mean herbage K decreased from 1.09% on 30 June to 0.82% on 2 September, whereas herbage Ca increased from 0.37 to 0.56% for switchgrass, 0.35 to 0.44% for big bluestem, and 0.43 to 0.51% for Indiangrass. Herbage Mg of switchgrass and Indiangrass decreased on 2 September while concentrations remained the same in big bluestem.

**Index words:** Warm-season grasses, *Panicum virgatum* L., *Andropogon gerardi* Vitman, *Sorghastrum nutans* L. Nash, Forage quality, Forage mineral concentrations, K, Ca, Mg, Soil fertility, Harvest date.

## INTRODUCTION

Interest has developed during recent years in native, perennial, warm-season prairie grasses as summer pasture for beef cattle in humid regions of the United States. Although livestock producers are concerned with the level of mineral nutrients in a ration, few researchers have measured mineral concentrations in warm-season grass herbage.

Big bluestem (*Andropogon gerardi* Vitman) contains approximately 1.35% potassium (K) according to Jurgens (1974). Gerloff et al. (1964) determined mineral levels in summer collections of native plants in Wisconsin. They reported K levels of 0.60% for switchgrass (*Panicum virgatum* L.) from a single site, 0.99 to 1.23% for big bluestem from four sites, and 0.75 to 1.03% for Indiangrass (*Sorghastrum nutans* L. Nash) from two sites. Herbage magnesium (Mg) concentrations were 0.22% for switchgrass, 0.16 to 0.34% for big

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bluestem, and 0.75 to 1.03% for Indiangrass. Wali et al. (1973) reported 0.16% leaf Mg for unfertilized big bluestem in native stands at four collection sites in the Minnesota-North Dakota Red River Valley.

Waller et al. (1972) studied the variation in mineral levels of native, warm-season pastures in northern Oklahoma over a 15-year period. Big bluestem contained the greatest concentrations of calcium (Ca), followed by Indiangrass and switchgrass. They determined that Ca supplementation is an unnecessary expense when beef cattle are pastured on warm-season grasses. Moxon et al. (1951) in South Dakota and Williams (1953) in Nebraska also have concluded that warm-season grasses contain adequate Ca for livestock. This northern Great Plains region normally has relatively low precipitation when compared with much of the northcentral and eastern United States.

Nitrogen (N) fertilization has been shown to influence mineral composition of cool-season grasses (George and Thill, 1979; George et al., 1979; Thill and George, 1975), but less is known about the effect of N on mineral nutrient levels in warm-season grasses. Balasko and Smith (1971) reported that N fertilization increased both K and Mg concentrations of switchgrass. In Nebraska, Rehm et al. (1977) observed that N and P fertilization did not consistently alter K, Ca, or Mg concentrations of herbage from a warm-season pasture mixture.

This study was conducted to measure herbage cation concentrations of three perennial, warm-season grasses fertilized with N.

## METHODS AND PROCEDURES

A field study was conducted in 1976 to measure K, Ca, and Mg concentrations in the herbage of warm-season grasses grown with different levels of N fertilization. The experimental site was located on a Clarion loam (Typic Hapludoll) at the Agronomy and Agricultural Engineering Research Center 15 km west of Ames, Iowa.

Soil samples were collected on 28 April 1976 and analyzed by the Iowa State University Soil Testing Procedures (K. Eik. 1968. Testing Methods, Iowa State University Soil Testing Laboratory, Mimeograph). Soil-available P averaged  $34 \text{ kg} \cdot \text{ha}^{-1}$  and soil exchangeable K averaged  $152 \text{ kg} \cdot \text{ha}^{-1}$ . Average rates of  $25 \text{ kg} \cdot \text{ha}^{-1}$  P and  $50 \text{ kg} \cdot \text{ha}^{-1}$  K were applied to the experimental site on 7 May as triple superphosphate (0-46-0) and  $\text{K}_2\text{SO}_4 \cdot \text{MgSO}_4$  (0-0-22).

Nine grass species x N level treatments were arranged in a randomized complete block experiment with four replications. Grass species consisted of switchgrass, big bluestem, and Indiangrass seeded in 1971. Plot size was  $1.83 \times 3.66 \text{ m}$ . Starting in 1972, surface plant residue was burned off annually preceding the appearance of spring growth. Nitrogen treatments were broadcast as urea (45-0-0) at levels of 0, 75, and  $150 \text{ kg} \cdot \text{ha}^{-1}$  N on 22 May 1976 and again on 3 July 1976 after the first harvest.

Plots were harvested on 30 June at early heading for switchgrass, late boot for big bluestem, and early boot for Indiangrass. A second harvest was made on 2 September when all three grass species were in a vegetative stage. A Carter flail-type harvester was used to harvest a  $0.92 \times 3.16 \text{ m}$  strip within each plot. Herbage samples used for cation analysis were subsamples of the total harvested yield. This subsample represented the vegetative growth above the recommended 20-cm minimum grazing height for warm-season grass

pastures. Herbage subsamples were dried in a forced-air oven at 60°C, ground to pass a 40-mesh screen, and stored in sealed glass bottles for laboratory analysis.

Herbage cation concentrations were determined by using a nitric-perchloric acid digestion (Isaac and Kerber, 1971). Calcium and Mg concentrations of the digest were determined by using a Perkin-Elmer Model 303 Atomic Absorption Spectrophotometer. Potassium concentration was determined by using a flame photometer. All herbage cation concentrations are reported on an oven-dry basis.

The data were treated statistically by using an analysis of variance with orthogonal polynomials to perform single degree of freedom comparisons (Steel and Torrie, 1960). Treatment means were compared by Duncan's Multiple Range Test.

## RESULTS AND DISCUSSION

### Herbage K

Herbage K concentrations tended to be greatest for switchgrass and least for Indiangrass (Table 1). Differences among grass species were not significant ( $P = 0.05$ ), however, when averaged over N levels and harvest dates. A significant harvest  $\times$  species interaction was observed. Mean K concentrations of 1.15% for switchgrass, 1.09% for big bluestem, and 1.04% for Indiangrass were significantly different when herbage was harvested on 30 June (Table 2). Difference among grass species were not significant on 2 September, but the herbage of all three grass species contained less K compared with concentrations measured on 30 June.

Herbage K concentrations decreased during the growing season. When averaged over grass species and N levels, herbage K decreased from 1.09% on 30 June to 0.82% on 2 September. Dry soil conditions may have limited K uptake after the 30 June harvest date because precipitation was only 19% of normal between 30 June and 2 September.

Fertilization with N had little effect on herbage K at the 30 June harvest, although the average of 1.14% with 150 kg·ha<sup>-1</sup> N tended to be greater than the average of 1.07% K for both the check and 75 kg·ha<sup>-1</sup> N treatments. Herbage K on 2 September decreased significantly with N fertilization. Mean values were 0.94, 0.80, and 0.73% K for the check, 75, and 150 kg·ha<sup>-1</sup> N treatments, respectively.

In general, herbage K concentrations observed in this study were relatively low compared with values observed for cool-season grasses (George and Thill, 1979; George et al., 1979; Thill and George, 1975) but were similar to those reported by Gerloff et al. (1964) for summer collections of big bluestem and Indiangrass in Wisconsin. Herbage K concentrations for switchgrass in our study, however, were greater than the 0.60% as reported by Gerloff et al. (1964). Additionally, herbage K concentrations observed for big bluestem were considerably less than the 1.35% suggested by Jurgens (1974).

### Herbage Ca

Mean herbage Ca concentrations of 0.47, 0.46, and 0.47% for switchgrass, big bluestem, and Indiangrass, respectively, were not significantly

Table 1. Herbage cation concentrations of switchgrass, big bluestem, and Indiangrass. Data are averaged over replications, nitrogen levels, and harvest dates, 1976.

Grass species	K	Ca	Mg
		(%)	
Switchgrass	0.99a†	0.47a	0.43a
Big bluestem	0.96a	0.46a	0.33b
Indiangrass	0.92a	0.47a	0.22c

†Means in the same column not having common letters are significantly different ( $P = 0.05$ ) by Duncan's Multiple Range Test.

different (Table 1). These values are greater than those reported by Waller et al. (1972).

Nitrogen fertilization resulted in a significant linear increase in herbage Ca for each warm-season grass species (Table 2). This trend for switchgrass is similar to that reported by Balasko and Smith (1971) but is unlike many other grass species as reported in a review by Beeson (1946).

Most of the variation in herbage Ca was associated with harvest dates. Mean values were 31% greater on 2 September compared with those on 30 June. A highly significant ( $P = 0.01$ ) species  $\times$  harvest date interaction was observed. Switchgrass, big bluestem, and Indiangrass means for the 30 June harvest were 0.37, 0.35, and 0.43% Ca, respectively. Switchgrass Ca increased to 0.56% by 2 September, a level which was 51% greater compared with that observed on 30 June. Big bluestem and Indiangrass Ca concentrations of 0.44 and 0.51%, respectively, were 18 and 26% greater than concentrations on 30 June.

The highly significant N level  $\times$  harvest date interaction seemed to result primarily from a relatively large increase in herbage Ca from 30 June to 2 September (0.43 to 0.61%) for the 150 kg·ha<sup>-1</sup> N treatment. Comparable increases were 0.33 to 0.42% and 0.40 to 0.48% for the 0 and 75 kg·ha<sup>-1</sup> N treatments, respectively.

The species  $\times$  N level harvest date interaction was highly significant. When no N was applied, herbage Ca was greater for Indiangrass than for switchgrass and big bluestem on 30 June. Additionally, N fertilization increased herbage Ca of switchgrass and big bluestem but had no effect on Indiangrass. On 2 September, herbage Ca was greater for all three species when the 150 kg·ha<sup>-1</sup> N treatment was compared with 75 kg·ha<sup>-1</sup>. Indiangrass was the only species that had greater herbage Ca when the 75 kg·ha<sup>-1</sup> N treatment was compared with no applied N.

Table 2. Herbage cation concentration of switchgrass, big bluestem, and Indiangrass with nitrogen fertilization and two harvest dates, 1976.

Grass species	N level	K			Ca			Mg		
		30 June	2 Sept.	Mean	30 June	2 Sept.	Mean	30 June	2 Sept.	Mean
	(kg·ha <sup>-1</sup> )				(%)					
Switchgrass	0	1.18	1.00	1.09a†	0.26	0.50	0.38c	0.23	0.22	0.23c
	75	1.12	0.79	0.95b	0.40	0.53	0.47b	0.52	0.41	0.47b
	150	1.15	0.71	0.93b	0.46	0.65	0.56a	0.62	0.56	0.59a
	Mean	1.15a	0.83b		0.37b	0.56a		0.46a	0.40b	
Big bluestem	0	1.02	0.92	0.97a	0.31	0.39	0.35c	0.25	0.21	0.23c
	75	1.07	0.84	0.95a	0.35	0.42	0.39b	0.35	0.35	0.35b
	150	1.16	0.73	0.94a	0.39	0.52	0.46a	0.39	0.43	0.41a
	Mean	1.09a	0.83b		0.35b	0.44a		0.33a	0.33a	
Indiangrass	0	1.00	0.89	0.94a	0.43	0.38	0.41c	0.17	0.12	0.14b
	75	1.02	0.77	0.89a	0.44	0.49	0.47b	0.25	0.21	0.23a
	150	1.09	0.76	0.92a	0.42	0.67	0.55a	0.26	0.28	0.27a
	Mean	1.04a	0.81b		0.43b	0.51a		0.23a	0.20b	

† Means not having common letters are significantly different ( $P = 0.05$ ) by Duncan's Multiple Range Test. Comparisons are between two harvest dates or among three nitrogen levels, within species and cations.

## Herbage Mg

Herbage Mg concentration was greatest for switchgrass, intermediate for big bluestem, and least for Indiangrass (Table 1). Concentrations of 0.43% for switchgrass and 0.33% for big bluestem are relatively high compared with values reported by others (Balasko and Smith, 1971; Gerloff et al., 1964; Wali et al., 1973). A mean Mg concentration of 0.22% for Indiangrass, however, is considerably less than 0.75 to 1.03% as reported by Gerloff et al. (1964).

Fertilization with 0, 75, and 150 kg·ha<sup>-1</sup> N resulted in herbage Mg concentrations of 0.20, 0.35, and 0.42%, respectively, when averaged over grass species and harvest dates. Although the effect of greater N application was primarily a linear increase in herbage Mg, a slight curvilinear response was observed. Herbage Mg increased by 75% with the first 75 kg·ha<sup>-1</sup> N increment as compared with an additional increase of only 35% for the second increment. The observed increase in herbage Mg with N fertilization was more pronounced for switchgrass than for either big bluestem or Indiangrass (Table 2). Balasko and Smith (1971) also observed that N fertilization increased herbage Mg concentration of switchgrass.

Mean herbage Mg was 0.34% on 30 June and 0.31% on 2 September. Concentrations were greater on 30 June compared with 2 September for both switchgrass and Indiangrass but remained at 0.33% for both harvests of big bluestem. Although all harvest date interactions with species and N levels were statistically significant, they accounted for a relatively small part of total variation in herbage Mg and lacked agronomic importance.

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REPRODUCTIVE RESPONSE OF SOYBEANS  
TO SHORT DAY LENGTHS<sup>1</sup>

B. K. Lawrence and W. R. Fehr<sup>2</sup>

**ABSTRACT.** Our objective, for soybean breeding purposes, was to determine if the number of days required to produce a generation of soybeans (*Glycine max*) could be reduced by the use of day lengths shorter than 12 hours. Two strains of each of various Maturity Groups were grown in controlled environment chambers under day lengths of 4, 8, and 12 hours. The average number of days to beginning bloom was 34 for the 4-hour, 24 for the 8-hour, and 26 for the 12-hour day length. The average number of days to seed maturity was 95 for the 4-hour, 85 for the 8-hour, and 81 for the 12-hour day length. The results indicate that no reduction in generation time can be achieved by reducing the day length to less than 12 hours.

Additional index words: *Glycine max* (L.) Merrill, Flowering, Maturity, Generation advance.

## INTRODUCTION

Single-seed descent is widely used in soybean [*Glycine max* (L.) Merrill] breeding programs for inbreeding segregating populations in greenhouses and winter nurseries (Fehr, 1978). The method requires only a few seeds per plant each generation; therefore, procedures that reduce the time from planting to seed production are useful, even if they reduce seed production.

One technique for obtaining rapid seed production in soybeans is the use of short day lengths (Fehr, 1980). Subtropical and tropical environments provide about a 12-hour day during the entire year, under which genotypes of Maturity Groups IV or earlier produce mature seed within 90 days after planting.<sup>3</sup> We were interested in the possibility of obtaining an even shorter generation time by the use, through environmental control, of a day length of less than 12 hours.

The only data presently available for day lengths of less than 12 hours concern days from planting to flowering, not to seed maturation. Garner and Allard (1920) compared four cultivars grown in 5-, 7-, and 12-hour day lengths.

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<sup>3</sup> Maturity Groups range from 00 for genotypes grown in northern Minnesota to X for genotypes grown near the equator (Pohlman, 1979).

The maximum difference in days to flower for any cultivar under these differing day lengths was four days. Byth (1968) compared four cultivars of Maturity Group VIII under 8-, 10-, and 12-hour day lengths, 'Bienville' and 'Nanda' of United States origin, 'Mamloki' from Nigeria, and 'Avoyelles' from Tanganyika. There was no difference between cultivars or day lengths for days to flowering under the 8- and 10-hour days. Neither did a 12-hour day change the response of Bienville and Nanda, but the flowering of Mamloki and Avoyelles was delayed. Both the classic study of Garner and Allard (1920) and more recent reference to soybeans (Byth, 1968) suggest that day lengths of less than 12 hours may have little effect on reduction of generation time, but no studies have been made of the period from planting to maturity. The objective of our investigation, then, was to determine if the time from planting to maturity could be reduced by growing soybeans in day lengths shorter than 12 hours throughout the life of the plant.

## MATERIALS AND METHODS

The research was conducted on two planting dates in controlled environmental chambers at Iowa State University, Ames, Iowa, in 1979. Two strains from each Maturity Group 00 through X and two day-neutral strains (Polson, 1972; Guthrie, 1972) were employed (Table 1). They were compared with a "reference" strain, 'Biloxi,' chosen because of its widespread use in photoperiod investigations (e.g., Parker and Borthwick, 1939).

### First Planting

Three chambers were used for the study, one for each of the three day lengths, 4, 8, or 12 hours of light per 24-hour period. Photoperiod treatment was initiated before seedling emergence and continued until maturity. Light sources were a mixture of incandescent and fluorescent light. Photosynthetic photon flux density at the soil surface was  $600 \mu\text{E}/\text{s}^{-1}/\text{m}^2$ . The day length treatments were centered within a 12-hour period at  $31^\circ\text{C}$ . A  $22^\circ\text{C}$  temperature was maintained for the remaining 12 hours of the 24-period.

There were three replications of each strain per chamber in a randomized complete-block design. Four seeds of each strain were planted in a 14.5-cm tall x 10-cm diam. plastic pot filled with a 1 sand: 1 peat mixture by volume. Plants were selected for uniformity and thinned to one plant per pot after emergence. Pots were watered daily, and no fertilizer was added to the potting mixture before or after planting. Days after the cotyledon stage (VC) were recorded for each plant for the reproductive stages R1 and R8 and the vegetative stages on that date. Descriptions for the cotyledon stage and the reproductive stages from Fehr and Caviness (1977) are as follows.

VC = The unifoliolate leaves have unrolled sufficiently so that the leaf edges are not touching.

R1 = One open flower at any node on the main stem.

R8 = 95% of the pods that have reached their mature pod color.

### Second Planting

Procedures were the same as for the first planting except for exclusion of the 4-hour regime (under which flowering and fruiting were delayed in the first

Table 1. Mean number of days from the cotyledon stage (VC) to beginning bloom (R1) and maturity (R8) for two strains of each maturity group 00 through X, two day-neutral strains, and a reference strain, Biloxi (see text).

Strain	Maturity group	VC to R1			VC to R8		
		Day length <sup>a</sup>			Day length		
		4	8	12	4	8	12
.....Days.....							
Altona	00	29	23	22	77	75	71
Norman	00	39	22	24	94	75	73
Clay	0	33	21	20	96	81	80
Evans	0	30	21	21	92	82	76
Hark	I	31	23	20	105	83	78
Hodgson	I	31	23	21	94	89	82
Beeson	II	40	24	22	... <sup>b</sup>	96	91
Corsoy	II	41	21	22	107	82	88
Williams	III	31	25	23	90	91	86
Woodworth	III	28	23	23	99	85	84
Cutler 71	IV	30	23	22	110	92	83
Kent	IV	30	24	24	...	97	90
Essex	V	26	20	22	94	90	88
Hill	V	29	21	26	81	78	76
Lee 74	VI	29	20	25	96	83	81
Tracy	VI	27	21	23	96	82	77
Bragg	VII	32	21	25	98	88	88
Ransom	VII	30	23	25	109	99	90
Hutton	VIII	33	22	24	102	90	83
Cobb	VIII	24	19	26	101	96	84
Santa Rosa	IX	32	23	29	96	96	90
Jupiter	IX	46	37	39	106	92	...
PI 274454	X	60	38	63	102	84	...
PI 240664	X	50	32	39	103	...	...
PI 153212	D.N. <sup>c</sup>	38	24	22	83	66	66
Shinsei	D.N.	26	22	22	77	79	70
Biloxi	Ref. <sup>d</sup>	35	29	32	101	90	95
Mean <sup>e</sup>		34	24	26	95	85	81
LSD <sup>f</sup>		7.7	3.7	2.8	10.2	11.0	8.0

<sup>a</sup>The cultivar means are of three replications in the 4-hour day length and six replications in the 8- and 12-hour day length.

<sup>b</sup>Strain did not develop to R8 in 110 days, when the experiment was terminated.

<sup>c</sup>Day-neutral cultivar.

<sup>d</sup>Reference cultivar of maturity group VIII.

<sup>e</sup>Means include only those cultivars that matured in all day lengths.

<sup>f</sup>Least significant difference at the 0.05 probability level.

planting), and switching of the chambers used for the 8 and 12 hour treatments.

### Analysis of Data

Two analyses of variance were conducted for the data. The data for the first planting were analyzed to compare the 4-, 8-, and 12-hour day lengths. Any effect due to the use of different chambers was confounded with the effects of the different day lengths. The data of both the first and second plantings for the 8- and 12-hour day lengths were combined for the second analysis. Plantings were considered random effects; day lengths and cultivars were considered fixed effects. Differences among chambers were not confounded with the combined analysis of 8- and 12-hour day lengths because each chamber was used for each day length.

## RESULTS

Number of days from VC to R1 and VC to R8 were significantly ( $P < 0.01$ ) greater for the 4-hour than for the 8- or 12-hour day lengths. Plants in the 4-hour day treatment were less vigorous and were lighter green than those in the other two day lengths. The amount of photosynthesis during the 4-hour period seemingly was insufficient to sustain normal plant development.

There was a difference of only two days between the 8- and 12-hour day lengths for days from VC to R1 and four days difference from VC to R8 (Table 1). The observed differences between day lengths were not statistically significant.

All the cultivars of Maturity Groups 00 to VIII, except 'Corsoy,' matured earlier under the twelve hours of light than with eight or four hours of light. 'Jupiter' and two plant introductions of Maturity Group X did not mature in the 12-hour day length because of vigorous vegetative growth that could not be adequately supported with moisture available in the pots.

The plants developed from R1 to R8 in less time in the 12-hour day length (55 days) than in the 4- or 8-hour day length (61 days). Differences among strains for days to maturity were largely due to length of the period from R1 to R8 (Table 1). The maximum difference to R1 between the day-neutral strain and those of Maturity Groups 00 through VIII was only four days. The maximum difference for days to R8, however, was 25 days between PI 153212 and 'Beeson.' Length of the period from R1 to R8 was not directly related to Maturity Group of the strains. For example, 'Tracy,' of Maturity Group VI, had a shorter period from R1 to R8 than many of the strains from earlier maturity groups.

Day lengths did not influence number of nodes on the main stem per plant, except for the strains that did not mature in 110 days (see footnote b in Table 1). Otherwise, there was an average of eight nodes on the main stem per plant in the 12- and 4-hour day lengths and seven nodes per plant in the 8-hour day length.

## DISCUSSION

Our results show no advantage in using day lengths of less than 12 hours to reduce the generation time of soybeans of maturity groups 00 through

VII. The shortest day length of four hours caused flowering and maturity to be delayed. Garner and Allard (1920) observed a delay of flowering of two days when 'Mandarin,' a maturity group I cultivar, and 'Peking,' a maturity group IV cultivar, were grown under a 5-hour day length compared with a 12-hour day length. We observed a greater delay with a 4-hour day length than these authors, possibly because of the lesser illumination in the chambers than obtained under full sunlight in the field.

The response of cultivars of maturity groups VIII, IX, and X to short day lengths was less consistent than for cultivars of earlier maturity groups. For example, PI 274454 showed a 25-day hastening of flowering in the 8-hour day length in all replications of the experiment; however, 'Santa Rosa' had only a 6-day hastening of flowering in the 8-hour day length. Genetic variation for response to short days in cultivars of maturity group VIII also was observed by Byth (1968). The two cultivars of United States origin that he studied did not differ in days to flowering for 8-, 10-, and 12-hour day lengths, whereas the two cultivars of tropical origin flowered later under the 12-hour regime than when exposed to 8- and 10-hour day lengths.

Breeders working with genotypes of maturity groups VII or earlier in winter nursery or greenhouse programs with 12-hour day lengths will not be able to reduce the length of time for seed production by further shortening the day length.

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## GROWTH ANALYSIS OF GRAIN SORGHUM HYBRIDS<sup>1</sup>

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**ABSTRACT.** Relationships among growth parameters determined from sorghum (*Sorghum bicolor* L. Moench) experiments which spanned a range of genotypes and planting arrangements were examined from early-vegetative to mature-plant stages of growth. Average crop growth rates,  $\overline{\text{CGR}}$ , increased continuously from the early vegetative stage and reached maximum values just before anthesis. The hybrids tested accumulated vegetative dry-matter at essentially the same rate, but they differed in rate of dry matter accumulation during grain filling. Differences in  $\overline{\text{CGR}}$  associated with variations in row spacings, plant densities, and height genotypes tended to be greater during the vegetative stages of growth.

Differences in average net assimilation rate,  $\overline{\text{NAR}}$ , attributable to hybrids and to planting regimes most often were not significant. Plant density exerted the greatest effect on average specific leaf weight,  $\overline{\text{SLW}}$ , with low-density plots showing higher  $\overline{\text{SLW}}$  values. Differences in  $\overline{\text{SLW}}$  ascribable to row spacings and hybrid genotypes were less pronounced and usually were not significant.

Leaf area index, LAI, reached a peak at 50 to 60 days after planting, remained constant until 80 days past planting, then declined. The taller hybrid of a near-isogenic pair had significantly longer leaf area duration, LAD, than did its shorter counterpart. Collectively, the effects of plant densities and hybrid genotypes on LAI and LAD seemed greater than the effects of row spacings.

Additional index words: *Sorghum bicolor* L. Moench, Dry matter, Leaf area, Plant development.

## INTRODUCTION

Measured changes in plant architecture and in dry-matter accumulation throughout the entire growth period are needed for definite growth analyses. The use of specific growth parameters to describe the pathways of dry-matter production in plants was first initiated by crop physiologists near the beginning of this century.

Limited studies of the impact of different growth parameters on development of the sorghum (*Sorghum bicolor* L. Moench) plant have often involved but a single genotype or planting regime. Fischer and Wilson (1975b) investigated the effect of plant density on growth of sorghums and found more dry-matter accumulation at high plant densities. Differences among plant

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densities for crop growth rate, CGR, at early stages of development were correlated with differences in leaf area index, LAI, and its influence on the amount of radiation intercepted. Reduction of CGR after heading was associated with reductions in LAI and net assimilation rate, NAR. Similar conclusions for sorghum were reached by Tateno and Ojima (1973).

Goldsworthy (1970) examined the physiologic basis for the differences in yield of three tall, late-maturing, Nigerian varieties and a short, early-American sorghum hybrid under different row spacings and plant densities. The CGR of all late varieties had a similar pattern. The rate increased to a peak at about 40 days after planting, then decreased sharply to very low values at approximately 100 days after planting, and increased again as heads emerged. The decrease in CGR was attributed to low radiation levels at the time and loss of dry weight from decay of old leaves. The short hybrid showed an increase in CGR until heading and a sharp decline thereafter which was associated with declines in NAR and LAI. Row-spacing and plant-density effects on growth were greater at the early stages of development. CGR was slowest at the widest spacing because of a small LAI.

Krishnamurthy et al. (1973) measured NAR and leaf area duration, LAD, after head emergence in sorghum and reported that LAD was correlated significantly with grain yield but that NAR showed no association with yield. In a later report, Krishnamurthy et al. (1974) stated that high yield in sorghum was directly associated with high CGR, which in turn depends on high as well as long LAD and high NAR.

Experiments conducted by Fisher and Wilson (1957a) showed that stem dry weight in sorghums increased up to flowering and then decreased during grain filling. They concluded that part of this loss represented transfer of assimilates to the grain, because grain growth rate was greater than CGR during this period. Warsi and Wright (1973) and Jacques et al. (1975) reported similar findings with sorghum.

Growth analyses of a sorghum hybrid and its parents were made by Gibson and Schertz (1977). The hybrid had greater leaf area than its parents until one week before flowering and less leaf area than its parents thereafter. CGR of the hybrid was greater than that of either parent from emergence to panicle initiation, but NAR and relative growth rate, RGR, did not differ among genotypes. Yield superiority of the hybrid was attributed mainly to the combination of the high CGR of the female parent during grain filling with the effective conversion of dry matter to grain of the male parent.

Our study of trends and interrelationships among the growth parameters was devised to provide a better understanding of the impact of genetic and environmental sources of variation on plant development. The paper presents results from growth analysis experiments in sorghum that spanned an appreciable range of hybrid genotypes and planting regimes, and one in which growth parameters were measured from early-vegetative stages until the completion of plant growth.

## MATERIALS AND METHODS

Our data were obtained from experiments conducted at the Iowa State University Research Farm near Ames, Iowa.

### Experiment One

Sorghums were grown in 1977 with the plantings made later than usual (June 15), because of dry weather that prevailed until early summer. Conditions for growth, however, were favorable after planting, and plant development and stature appeared normal.

Plantings were arranged in a split-plot design, with row spacings randomized as whole plots and a  $2 \times 2$  factorial combination of hybrids (tall and short) and plant densities (low and high) randomized as subplots, with three replicates of each plot type. Rows were spaced 51, 76, or 102 cm apart, and plant densities were 128 and 256 thousand plants/ha. The genotypes tested were near-isogenic hybrids, 'A, Combine Kafir 60'  $\times$  'Tx7078' (the "tall" hybrid) and 'A, Tx616 Kafir'  $\times$  'Tx7078' (the "short" hybrid). Genetically, the tall hybrid is homozygous dominant at height locus 2 ( $Dw_2Dw_2$ ), the short hybrid is heterozygous ( $Dw_2dw_2$ ), and both hybrids are homozygous-recessive at the other major height loci (Quinby and Karper, 1954). Each experimental unit (plot) consisted of three rows 6.1 m long, and each unit was replicated three times.

Data were obtained for leaf area and plant dry weight from early vegetative stage until plants were approaching maturity. Beginning at 30 days after planting and continuing each ten days thereafter until 70 days after planting, ten consecutive plants in each plot were pulled from the soil and the roots discarded. Five plants per plot were sampled at 80, 90, and 100 days after planting. Leaves were detached from the plants, and their areas were measured individually by using a Licor Model LI3000 portable area meter. Total-plant dry weights also were obtained from the same number of plants at each sampling period, except that 20 plants per plot were taken at 30 days after planting.

### Experiment Two

Sorghums were planted on May 26, 1978. The entries were ten hybrids that span the range, both for agronomic characteristics and for diversity of commonly used male and female parents, that is available in grain sorghum hybrids. The row spacing was 102 cm, plant density was 128 thousand plants/ha, and the entries were arranged in a randomized complete-block design with three replicates. Plots were single rows 4.3 m long, with ten plants sampled at 40, 60, 80, and 100 days after planting, respectively. Leaf area measurements and plant dry weights were obtained in the manner described for Experiment One. Plants were vigorous, and the mean grain yield for the ten hybrids in an adjacent three-replicate test was 75 q/ha.

### Calculation Definitions

Leaf area and plant dry weight data from each experiment were used to calculate the following growth functions, using formulas derived by Radford (1967):

$\overline{\text{CGR}}$ . Average crop growth rate; i.e., the average increase in plant dry weight per unit of land area per unit of time.  
 $= W_{t_n + 1} - W_{t_n} / t_n + 1 - t_n$ , expressed as  $\text{g/m}^2/\text{day}$ .

$\overline{\text{NAR}}$ . Average net assimilation rate; i.e., the average increase of plant dry weight per unit of leaf area per unit of time.  
 $= [W_{\text{tn}+1} - W_{\text{tn}} / A_{\text{tn}+1} - A_{\text{tn}}] [\log_e A_{\text{tn}+1} - \log_e A_{\text{tn}} / \text{tn} + 1 - \text{tn}]$ , expressed as  $\text{g}/\text{dm}^2/\text{day}$ .

$\overline{\text{SLW}}$ . Average specific leaf weight; i.e., the amount of leaf dry weight per unit leaf area.  
 $= \frac{1}{2} (LW_{\text{tn}} / A_{\text{tn}} + LW_{\text{tn}+1} / A_{\text{tn}+1})$ , expressed as  $\text{g}/\text{dm}^2$ .

$\text{LAI}$ . Leaf area index; i.e., the ratio of leaf area to unit land area.  
 $= A_{\text{tn}} / \text{unit land area at tn}$ .

$\text{LAD}$ . Leaf area duration; i.e., the duration of active leaf area over time.  
 $= \sum_{i=1}^n A_i$ , expressed as  $\text{dm}^2$ .

where:

$W$  = total plant dry weight per  $\text{m}^2$

$A$  = leaf area ( $\text{dm}^2$ )

$LW$  = leaf dry weight per  $\text{m}^2$

$t$  = time in days

$n$  = number of sampling intervals  $n = 1, 2, \dots, 8$ .

## RESULTS AND DISCUSSION

A tabulation of the sampling intervals and stages of plant development that were used in the calculation of growth parameters is presented in Table 1. The vegetative stage includes leaf growth, stem growth, and differentiation of the fruiting (panicle) structure. Anthesis embraces the period of continuing panicle growth, pollen shedding, fertilization, and stem growth. Grain filling includes the completion of stem growth and the period of rapid increase in dry weight of the grain.

Interactions between the main effects in Experiment 1 were significant ( $P < 0.05$ ) in only a very few instances for any of the growth parameters. The discussion, therefore, will be concerned with only main treatment effects for  $\overline{\text{CGR}}$  and the other growth parameters.

For the hybrids grown in Experiment 1 (Table 2),  $\overline{\text{CGR}}$  increased from the early vegetative stage to Interval 4 (just before anthesis), decreased to Interval 6 (beginning of grain filling), and again increased during the grain filling period (Interval 7). This pattern of growth is similar to that observed for tropical maize varieties by Goldsworthy and Colegrove (1974) and Goldsworthy et al. (1974). They found that crop growth rate increased to a maximum at silking, then declined steadily.

Differences among row spacings in  $\overline{\text{CGR}}$  were significant only in Intervals 1 and 3, with the highest values obtained for the 76-cm row spacing. During the vegetative stage,  $\overline{\text{CGR}}$  was highest in the 76-cm row width. This

Table 1. Sampling intervals and developmental stages for growth analysis calculations.

Sample number	Days after planting	Sampling interval	Development stage
Experiment 1			
1	30	1	Vegetative
2	40	2	
3	50	3	
4	60	4	
5	70	5	Anthesis
6	80	6	Grain filling
7	90	7	
8	100		
Experiment 2			
1	40	1	Vegetative
2	60	2	Anthesis
3	80	3	Grain filling
4	100		

was not true during most of anthesis, but  $\overline{\text{CGR}}$  was again highest in 76 cm row widths during the later part of the grain filling period. During a major portion of the growth cycle (Intervals 1 through 5),  $\overline{\text{CGR}}$  was significantly greater at the high plant density. But, during grain filling, significant differences in  $\overline{\text{CGR}}$  between plant densities were not detected. The greater  $\overline{\text{CGR}}$  during the vegetative phase in the high density plantings may have been simply due to the larger number of plants per unit land area. During grain filling, however, the rate of accumulation of dry matter per plant at the low density was evidently greater than those competing at the high density. Consequently, significant differences in  $\overline{\text{CGR}}$  were not observed in Interval 7.

Although the differences were significant only in Intervals 1 and 3, the taller hybrid exhibited consistently higher  $\overline{\text{CGR}}$  during the entire vegetative growth phase (Intervals 1 through 5). A distinct pattern in  $\overline{\text{CGR}}$  during grain filling was not evident. This suggests that the homozygous dominant condition of height locus 2 ( $Dw_2Dw_2$ ) had an enhancing effect on rate of vegetative growth, but it did not have a significant effect on rate of dry-matter accumulation during grain filling.

Table 2. Effects and significance levels of row spacings, plant densities, and height genotypes (hybrids) on mean crop growth rate ( $\text{g/m}^2/\text{day}$ ), Ames, Iowa, 1977.

Treatments	Sampling intervals						
	1	2	3	4	5	6	7
Spacings							
51 cm	12.4	18.0	23.6	23.5	20.8	3.0	18.6
76 cm	12.9	20.2	29.6	34.8	12.3	0.0	32.2
102 cm	10.5	16.0	20.4	33.1	9.7	6.6	22.1
Significance†	*	NS	**	NS	NS	NS	NS
Densities							
Low	10.1	15.0	23.9	24.2	7.5	1.9	23.3
High	13.8	21.1	25.2	36.7	21.0	4.1	23.3
Significance	**	**	NS	**	*	NS	NS
Hybrids							
Short	10.9	17.0	20.9	27.0	10.3	8.1	23.2
Tall	13.0	19.1	28.2	33.9	18.3	0.0	25.3
Significance	**	NS	*	NS	NS	NS	NS
C.V., %	13.7	26.4	31.1	40.4	74.7	58.6	50.4

†, \*, \*\* Significant at  $P < 0.05$  and  $P < 0.01$ , respectively; NS = not significant.

Table 3. Average crop growth rate ( $\text{g/m}^2/\text{day}$ ) over three sampling intervals for ten hybrids, Ames, Iowa, 1978.

Hybrids	Sampling intervals		
	1	2	3
NB 505	19.8	11.7	15.4
RS 506	20.1	14.7	12.7
RS 610	20.5	13.2	21.5
RS 628	22.8	16.5	8.7
RS 633	18.7	15.9	21.8
TX 680	22.0	21.4	19.6
RS 690	18.2	14.6	19.2
KS 692	18.0	14.9	20.2
W 832	20.5	18.0	15.7
W 866	17.6	20.0	22.6
LSD <sub>0.5</sub>	NS	NS	8.3
C.V., %	16.2	36.0	28.5

Variations in  $\overline{\text{CGR}}$  among the diverse hybrids of Experiment 2 (Table 3) indicated that they accumulated vegetative dry matter at essentially the same rate, but they differed in rate of dry-matter accumulation during grain filling. Often the hybrids showed relatively large  $\overline{\text{CGR}}$  values in Interval 1 (vegetative phase); then the values decreased during Interval 2 (anthesis), and the rate increased again in Interval 3 (grain filling). However, some hybrids did not follow the general pattern. RS628 showed a continuous decrease in  $\overline{\text{CGR}}$  from Intervals 1 through 3, and Tx680 displayed an essentially constant  $\overline{\text{CGR}}$  during most of the growing season.

Differences in  $\overline{\text{NAR}}$  associated with the treatments of Experiment 1 and the diverse hybrids grown in Experiment 2 usually were not significant ( $P < 0.05$ ).  $\overline{\text{NAR}}$  values ranged largely between 0.028 and 0.096  $\text{g/dm}^2/\text{day}$  for the different sampling intervals, with coefficients of variation for this character being slightly higher than those shown for crop growth rate.

One might expect that plants grown in the narrower rows would have greater potential for photosynthesis, because of better spatial distribution of plants within the same land area and, therefore, more efficient light utilization. Our experiment, however, showed similar  $\overline{\text{NAR}}$  values at all row spacings. The hybrids, particularly the short one, have their leaves quite close together and may have leaf orientations that are not adequate to fully exploit all the sunlight available. It may be that most photosynthesis at all row spacings took

Table 4. Effects and significance levels of row spacings, plant densities, and height genotypes (hybrids) on mean specific leaf weight ( $\text{g}/\text{dm}^2$ ), Ames, Iowa, 1977.

Treatments	Sampling intervals						
	1	2	3	4	5	6	7
Spacings							
51 cm	0.374	0.439	0.487	0.517	0.533	0.524	0.501
76 cm	0.370	0.417	0.467	0.497	0.512	0.508	0.496
102 cm	0.360	0.411	0.464	0.494	0.516	0.520	0.493
Significance†	NS	**	*	NS	NS	NS	NS
Densities							
Low	0.383	0.435	0.497	0.528	0.542	0.545	0.528
High	0.354	0.409	0.449	0.477	0.499	0.491	0.465
Significance	**	**	**	**	**	**	**
Hybrids							
Short	0.372	0.424	0.474	0.503	0.517	0.512	0.489
Tall	0.365	0.421	0.471	0.503	0.523	0.523	0.504
Significance	NS	NS	NS	NS	NS	NS	NS
C.V., %	7.4	3.9	4.7	4.4	3.3	3.7	5.2

†, \*, \*\* Significance at  $P < 0.05$  and  $P < 0.01$ , respectively; NS = not significant.

place in the upper leaves of the canopy, which were fully exposed to light at all spacings.

Significant differences in  $\overline{\text{NAR}}$  were obtained only during Intervals 1 and 3 for plant densities and between the hybrids. The low density showed a larger mean in these instances with decreased leaf shading a possible factor responsible for the higher values. The tall hybrid displayed higher  $\overline{\text{NAR}}$  values during vegetative growth, but the advantages were significant ( $P < 0.05$ ) only in Intervals 1 and 3. Net assimilation rates during grain filling were similar for both hybrids.

The ten hybrids in Experiment 2 did not differ significantly ( $P < 0.05$ ) for  $\overline{\text{NAR}}$  in any of the sampling intervals. Variations among the hybrids, however, were similar to those discussed for  $\overline{\text{CGR}}$ . Highest  $\overline{\text{NAR}}$  values were obtained for all but one hybrid during the vegetative phase; then they decreased during anthesis. The values increased again during grain filling, but they did not reach the level which had been attained during the vegetative stage. The exception again was RS628, which showed a continuous decrease from Intervals 1 through 3.

Specific leaf weights in Experiment 1 (Table 4) increased from Intervals 1 through 5 (vegetative growth and anthesis) and then decreased from Intervals 6 to 7 (grain filling). Because there was little or no increase in leaf area after Interval 2, the increase in  $\overline{\text{SLW}}$  after this period may be attributed to accumulation of dry matter in the leaves. This indicates that photosynthesis during the vegetative phase was more than adequate to satisfy the needs of all growing parts (leaves, stems, and panicles), and (or) that the transport system was not able to translocate all synthesized material to the active sinks. If one assumes that the transport system was not limiting the translocation of assimilates (Fisher and Wilson, 1975a), then assimilate supply should not have been a limiting step for spikelet differentiation.

The decrease in  $\overline{\text{SLW}}$  observed at Intervals 6 and 7 coincided with rapid grain growth. Although the decrease was not great, it seemed to indicate that some transport of stored materials from leaves was occurring. The translocation of assimilates from the leaves may not have made a large contribution to grain growth, but it served to indicate that photosynthesis during grain filling may not have provided enough assimilates to completely fill all the differentiated grains to capacity.

Specific leaf weight usually was highest in the 51-cm row spacings, followed by 76- and 102-cm row widths, respectively. The differences were significant, however, only in Intervals 2 and 3. But the differences in  $\overline{\text{SLW}}$  between plant densities were significant ( $P < 0.05$ ) at all sampling intervals. Plants in the lower density had higher  $\overline{\text{SLW}}$  values in all instances. This advantage may have resulted from excess photosynthesis, promoted by better light utilization. The fact that  $\overline{\text{SLW}}$  values for the tall versus short hybrid did not differ significantly at any sampling interval indicates that the allelic structure at height locus 2 seemingly had little or no influence on the amount of photosynthates accumulated in the leaves.



Table 5. Average specific leaf weight ( $\text{g}/\text{dm}^2$ ) over three sampling intervals for ten hybrids, Ames, Iowa, 1978.

Hybrids	Sampling intervals		
	1	2	3
NB 505	0.497	0.551	0.579
RS 506	0.482	0.506	0.544
RS 610	0.482	0.513	0.525
RS 628	0.489	0.519	0.525
RS 633	0.473	0.525	0.547
TX 680	0.501	0.529	0.539
RS 690	0.482	0.522	0.545
KS 692	0.492	0.538	0.566
W 832	0.472	0.499	0.509
W 866	0.487	0.513	0.539
LSD <sub>0.5</sub>	NS	0.029	0.039
C.V., %	3.56	2.31	3.03

A continuous increase in  $\overline{\text{SLW}}$  was observed from the vegetative through grain-filling stages in Experiment 2 (Table 5). Because leaf area expansion was completed at the end of Interval 1, the later increases must have been generated by the accumulation of dry matter in the leaves. Significant differences ( $P < 0.01$ ) in  $\overline{\text{SLW}}$  among hybrids were observed only during Intervals 2 and 3 indicating that this group of hybrids differed in their ability to accumulate dry matter in the leaves after anthesis but not before.

Leaf area index in Experiment 1 increased to a peak at 50 days after planting. After remaining essentially constant for some additional 20 days, there was a gradual decrease at 80 and 90 days, then a more rapid decrease to 100 days due to senescence of the lower leaves (Table 6). Significant differences in LAI among row spacings were detected at all sampling intervals, except 30 days past planting. Leaf area index was highest at the 76-cm row width, followed by the 51- and 102-cm row spacings, respectively. This ranking was surprising because one would expect the LAIs to be largest at the narrowest row spacing. The rankings observed probably resulted because the actual or effective plant populations after thinning were slightly lower than the prescribed levels at the 51- and 102-cm row widths but slightly higher than the prescribed levels at 76-cm row spacing. This was true for both the low and the high densities. The proportionately greater number of plants at the 76-cm row width may have inflated the LAI values somewhat for that spacing.

Table 6. Effects and significance levels of row spacings, plant densities, and height genotypes (hybrids) on mean leaf area index at each sampling interval, Ames, Iowa, 1977.

Treatments	Days after planting							
	30	40	50	60	70	80	90	100
<b>Spacings</b>								
51 cm	0.68	2.38	3.67	3.63	3.68	3.55	3.64	3.32
76 cm	0.72	2.62	4.15	4.31	4.16	4.09	3.91	3.83
102 cm	0.57	2.11	3.40	3.33	3.51	3.40	3.41	3.24
Significance†	NS	**	**	*	**	**	*	**
<b>Densities</b>								
Low	0.49	1.86	2.95	3.01	2.95	2.85	2.80	2.69
High	0.83	2.88	4.53	4.51	4.63	4.51	4.52	4.21
Significance	**	**	**	**	**	**	**	**
<b>Hybrids</b>								
Short	0.63	2.27	3.54	3.56	3.60	3.47	3.50	3.26
Tall	0.68	2.47	3.94	3.96	3.97	3.89	3.81	3.64
Significance	NS	**	**	**	**	**	**	**
C.V., %	15.2	7.5	8.2	10.5	7.3	6.4	7.0	6.7

†, \*, \*\* Significant at  $P < 0.05$  and  $P < 0.01$ , respectively; NS = not significant.

Table 7. Mean leaf area index at four sampling intervals for ten hybrids, Ames, Iowa, 1978.

Hybrids	Days after planting			
	40	60	80	100
NB 505	1.74	3.37	2.48	2.28
RS 506	1.89	3.70	2.33	2.00
RS 610	1.80	3.77	3.17	3.10
RS 628	1.68	5.34	4.45	3.44
RS 633	1.73	3.92	3.70	3.54
TX 680	1.54	4.18	4.12	3.51
RS 690	1.88	4.14	3.91	3.43
KS 692	1.43	3.94	3.07	2.98
W 832	1.63	4.84	4.29	3.77
W 866	1.66	3.80	3.58	3.47
LSD <sub>.05</sub>	NS	0.97	0.49	0.57
C.V., %	19.1	13.8	8.1	10.6

Differences in LAI between plant densities were significant ( $P < 0.01$ ) at all sampling intervals (Table 6). Higher LAIs were observed at the high density because of the increased number of plants per unit land area. The LAI values for the two hybrids were significantly different ( $P < 0.01$ ) at all sampling intervals, except 30 days after planting. Larger LAIs were associated with the tall hybrid. This indicates that the heterozygous state of height locus 2 had a reducing effect on the development of plant leaf area. Inasmuch as leaf numbers were similar for the two hybrids, the advantage in leaf area for the tall hybrid must have been due to larger leaves. LAI differences among the ten hybrids in Experiment 2 were not detected at 40 days after planting, but significant differences were observed thereafter (Table 7). Leaf area index values were highest at 60 days after planting and declined at the later sampling intervals.

Genotypes that have a long duration of growth may be as productive as others that may be more efficient in producing dry matter. In Experiment 1, the tall hybrid had significantly ( $P < 0.01$ ) larger LAD values than did the short hybrid at all sampling intervals (Table 8). This difference was due to greater leaf area production by the taller hybrid during all intervals.

Production practices also may influence leaf area duration in sorghums. The effects of row spacings on LAD values were significant ( $P < 0.01$ ) at all sampling intervals in Experiment 1. Values for duration of leaf area were largest at the 76-cm row widths, followed by those for the 51- and 102-cm

Table 8. Effects and significance levels of row spacings, plant densities, and height genotypes (hybrids) on mean leaf area duration ( $\text{dm}^2/\text{m}^2$ ), Ames, Iowa, 1977.

Treatments	Sampling intervals						
	1	2	3	4	5	6	7
Spacings							
51 cm	306	673	1036	1398	1753	2118	2446
76 cm	334	749	1181	1597	2007	2368	2784
102 cm	268	608	933	1285	1624	1966	2289
Significance†	**	**	**	**	**	**	**
Densities							
Low	234	529	826	1120	1406	1685	1954
High	371	824	1275	1733	2184	2616	3056
Significance	**	**	*	*	*	**	**
Hybrids							
Short	290	644	995	1350	1697	2027	2373
Tall	315	709	1106	1503	1892	2274	2638
Significance	**	**	**	**	**	**	**
C.V., %	7.4	8.2	10.0	8.9	6.4	7.1	6.7

†, \*, \*\* Significant at  $P < 0.05$  and  $P < 0.01$ , respectively; NS = not significant.

Table 9. Average leaf area duration ( $\text{dm}^2/\text{m}^2$ ) over three sampling intervals for ten hybrids, Ames, Iowa, 1978.

Hybrids	Sampling intervals		
	1	2	3
NB 505	511	759	987
RS 506	559	792	992
RS 610	556	873	1183
RS 628	702	1146	1490
RS 633	564	934	1288
TX 680	571	983	1333
RS 690	601	992	1335
KS 692	536	844	1142
W 832	647	1075	1453
W 866	545	903	1251
LSD <sub>.05</sub>	NS	142	200
C.V., %	12.4	8.9	6.8

row spacings, respectively. The advantage in LAD for the 76-cm row spacing was due to larger leaf area index at that spacing at all sampling intervals. Significantly larger LAD values likewise were observed at the high plant density at all samplings. Larger LAIs at the high density again were responsible for the advantage. Collectively, the effects of plant densities and hybrids on LAI and LAD seemed greater than the effects of row spacings on these parameters.

Significant differences in LAD among the contrasting hybrids of Experiment 2 were detected only in Intervals 2 and 3 (Table 9). The values were smallest for the very early-maturing hybrids, NB505 and RS506; otherwise, there was no association of LAD with readily discernable plant characteristics.

Analyses of variance for some of the growth parameters determined in our experiments showed rather large coefficients of variability, beyond 20 or 30%. This was particularly true for  $\overline{\text{CGR}}$  and  $\overline{\text{NAR}}$  and for the anthesis and early grain filling stages. Large differences between treatments or entries were needed, therefore, to meet the conventional probability levels that indicate a real difference. Many of the relationships presented seem distinct, and they meet statistical tests for significance. But others are less clear; thus, our discussions and conclusions must be based largely on trends rather than sharp differences. As interest in growth analyses of crop plants accelerates, it is hoped that improvements in the techniques and precision of quantifying growth functions

will evolve. Such improvements, together with additional studies that examine the impact of genotypic and environmental variables on the expression of growth parameters, should help plant scientists attain a more complete and precise understanding of plant growth and development.

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## LA CHAGALLITÉ: THE STYLE IN TAPESTRY

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**ABSTRACT.** A commissioned work by Marc Chagall hangs in the Helfaer Center in Milwaukee, Wisconsin. It is the only tapestry by Chagall in this country. At a time when artists' works are being funded as one percent of the cost of new federal buildings, this art work exemplifies support by private donors. The complex of buildings which form the Jewish Community Center known as the Helfaer Center unifies social and artistic dimensions which create an enviable atmosphere for the diverse services within the complex. The donor's vision in providing a master work has also added to growing visual enhancements of the city. The events surrounding the tapestry and its symbolism are described, including the presence of Golda Meir in the tapestry itself.

Additional index words: Chagall, Tapestry, Helfaer Center, Edward Durrell Stone, Golda Meir.

As a world figure in art, Marc Chagall, at 95, has outlived Matisse, Braque, and Picasso, all of whom enriched his artistic thought during the Paris years. In Paris Chagall lived at the "beehive" studio, La Ruche, with the poets, Cendrars and Apollinaire. They called him "surreal." There he came into full possession of an artistic integration of his prior experience. His idiom of expression was formed neither entirely from the folk art and decorative boldness of his rural Russian ties, nor entirely from the cross-currents of new ideas and the innovations of cubism associated with his sophisticated Parisian ties. Since 1966 he has been living in St. Paul de Vence at "La Colline," a short walk from Matisse's famous chapel at Vence. His work day begins at ten in the morning and ends at ten at night. Chagall carries a large key to his atelier which admits himself and one other, his wife, Valentina, or "Vava."<sup>1</sup>

In his late years, like Picasso, Chagall has created pottery, sculpture, stained glass, mosaic, and tapestry. Three of his tapestries hang in the Knesset in Israel and one in the United States. The one in this country is a 14 by 19 foot handwoven wool tapestry commissioned in 1972 for Evan Helfaer in memory of his wife, Marion, for the atrium in the Helfaer Community Service Building, which is part of a complex at 1360 Prospect Avenue in Milwaukee, Wisconsin.

Created as a small gouache painting, which is a water-based opaque medium, the tapestry was later woven in the Paris atelier of Yvette Cauquille-Prince. Chagall does not pattern a tapestry after an existing painting. He makes a maquette, a small, original drawing, or a gouache, or works from an earlier lithograph. Mme. Prince says, "If Chagall starts a sentence, I can finish it. And so, when I see his gouache, I know exactly what he wants."<sup>2</sup> The imagery and color of the gouache form the single source from which she works. The result is a masterful translation of tonal relationships and color that reveal her rapport and respect for the artist. A painter turned weaver, Mme. Prince trained at the Musée des Beaux Artes in Paris. Her taste has developed from the Coptic style, some two thousand years old, and the source of Gothic tapestry, rather than by

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nineteenth century imitations of paintings, technically proficient, but as she believes, "très mauvais."

The weaver does exist in the unique idiomatic texture of the detail. To be "tout création Chagall" Mme. Prince's translation needed "love and total comprehension. I am like a conductor, and Chagall is the music. I must understand the work of Chagall so perfectly that I myself do not exist," she has said. Furthermore, she has remarked, "I look at it for a long time. . . six weeks. . . until I understand. Then I return to Chagall's house and I say, 'Like this? Like that?' He will say, 'D'accord! Exactly!' After the weaving is begun, Chagall will come for the pleasure and the beauty, and for this reason only. He trusts me."<sup>3</sup>

In thinking a painting into wool, the weaver redraws a cartoon on the reverse side of linen to the full size of the tapestry. Holding strands of colored wool in one hand and pencil in the other, she uses her own invention, a numbered code, "tout comptes," a chart which Turkish and Moroccan weavers in her atelier follow. In seven years she has perfected her technique and code. She travelled to the Moroccan village of Meknes to buy special wool spun and dyed to her formulae and approved by Chagall. To interpret his brush strokes in wool, she used other wool from France and Australia with different degrees of roughness to change surface textures. Certain areas, such as the eyes of the major figure, the prophet, she wove herself. So faithful was the weaver to the artist's maquette that any sign of displeasure with the tapestry from Chagall meant that it would be destroyed when it was cut from the loom.

Coptic textiles have found their way into museums since 1884 when Gaston Maspero discovered some burial grounds in the low sand hills east of Akhim in Upper Egypt.<sup>5</sup> They date from the fourth to the twelfth centuries. These textiles were most certainly not woven in factories but in cottages, and domestic work of this sort resists exact classification. It reflects essentially the provincial taste in a period of national Christian revival of a people accustomed to a long Greek occupation and, successively, Roman, Persian, and Arab rule. The word from the Greek "Agytios" for "Egypt" became the Arabic "Kibt" and was Christianized to "Copt."<sup>6</sup> Stylistically, Coptic is an art of rural people far from the sophistication of Alexandria with its Hellenistic outlook. Chagall's work echoes the folklore of the ancient Coptic time. The polychromy, the distortions in form, the portrayals combining plant, animal, figure, and floral sprays are parallels to Coptic imagery.

The weaving is also characteristic of Coptic technique. The woven surface is solid-weft-faced, ranging from a tough solidity of surface to coarseness of effect. These wefts are rarely carried the full width of the web. Only where a color appears in the design is a weft of this color inserted back and forth to completely cover the warp in that unit, forming marked parallel ridges. They are pushed tightly together by battens, reeds, or combs. If a color is parallel to the warp at a margin, a slit is formed. If not parallel, the warp dovetails into the weft, or a single weft can alternate and a sawtooth-clustering can be effected at one side or both.

Historically, the words "tapis," rug, and "tapisserie," tapestry, are somewhat ambiguous in describing these coverings for furniture, wall, or floor. The medieval "arras" was used in Shakespeare's time, when Paris, Arras, and Aubusson were renowned weaving centers. One hundred fifty thousand weavers worked at a time when the population was one-tenth the size of modern Europe. A weaver might complete two or three tapestries in a lifetime,

and the laborious task of matching colors was achieved entirely by eye discrimination. Aubusson and Gobelins have endured to modern times. They created flat, mural effects in Gothic times using only 14 shades of colors, but in the 19th century the art so mimicked painting that the weavers could match the 14,000 hues charted by Michel Chevreul, the director of dyes at Gobelins.

The modern revolution in tapestry in 1930 was led by Mme. Cuttoli who broke away from the great houses of France. She commissioned Picasso, Matisse, Miro, Leger, and Le Corbusier to submit oil paintings for cartoons for her weavers to execute. By 1936 she had 16 to exhibit around the world.

One of the modern French painters, Jean Lurçat (1892-1966), along with Mme. Cuttoli, revived both the art and business of tapestry at Aubusson in 1933. It was Lurçat who, from a painter's perspective, picked up the lapsed aesthetic of tapestry. He redirected his own art as he watched his wife work at petit point and, as an artist-artisan, began embroidering and weaving fabric and rugs himself.<sup>7</sup>

Chagall's tapestry is in the spirit of this modern revival. He was aware of a tapestry's "covering" quality to fit a wall space as a flat mural, of the taste to avoid modelling renditions of depth and perspective, of the use of restricted color gradations and juxtaposed opaque colors, and of the need to employ coarse weave to modulate the surface texture. Chagall said, "I had to wait until I was an old man . . . before I understood the importance of texture."<sup>8</sup> Mme. Prince calls her interpretation of the classic technique, "weaving with the form, from the inside . . . it is done in reverse, upside down and backwards. You really cannot see what you are weaving until the tapestry is completed."

In 1965, when Chagall's Kneset tapestries were begun at Gobelins, Chagall went to Rome to study those of Raphael in the Vatican. In preparation for the weaving of the tapestry, a color circle of 160 colors of dyed yarns was prepared for him by Maurice Couchy, the head of the Manufacture des Gobelins. Later the circle was reduced to 110 tones of which only half were used enough to be considered important to the tapestry. Chagall's drawing style, a "loose handwriting," and his light and shade were modified to more appropriately translate them into tapestry. In a search for brilliance of tones, Chagall entered into the realm of weavers to find solutions and to learn about weaving.<sup>9</sup> In 1969 Chagall encountered Mme. Prince who had woven for Klee and Picasso and said, "She's the one for me." An enduring partnership and friendship began.

There is only one tapestry of the Milwaukee Chagall. Modern tapestries are priced by size and by the reputation of the artist. Both French and United States law limit the number of copies of any tapestry design to six, plus two artist's proofs in order to qualify as an original work of art. If very large, only one tapestry may be permitted to be woven.<sup>10</sup> In the great house of Gobelins, private commissions are not taken, only public transactions.

The Milwaukee Chagall tapestry is also significant and symbolic as a private donor's gift to a social institution. The building in which it is housed is equally auspicious. Evan Helfaer, the late Milwaukee philanthropist, saw his community center completed and the Chagall tapestry dedicated in 1973. Helfaer had built Lakeside Laboratories, a pharmaceutical firm in Milwaukee. His gifts to health care, youth recreation, theatre, and music were crowned by the center. Designed by Edward Durrell Stone, it is part of a three-building complex. In it are housed the Jewish Federation offices, Vocational service,

Family and Children's services, Career and Counseling services, the Anti-Defamation League, the B'nai B'rith Youth Organization, the Milwaukee Jewish Council, and the Wisconsin Jewish Chronicle.

Interconnecting corridors link this southernmost building to the Jewish Community Center, built in 1954 for recreation and education, and the Jewish Home for the Aged, built in 1974. Melvin Zaret, the director, describes the orchestration of the concept as, "beauty in services rendered. The wings where we serve the needs of older and younger people are interconnected, so each group will learn from the other. Children do not fear aging and their elders welcome companionship. Functionally, it becomes easier for them to communicate, cooperate and interchange ideas."

Jordan Miller of Miller, Waltz Diedrich, Milwaukee Associates working with Stone's firm felt that despite variances the buildings were compatible as an integrated environment. "Each can use each other's facilities. The older folk can mingle with children and families in the center, with its restaurant, swimming pool, exercise equipment, and meeting rooms."<sup>11</sup>

The guidon role in this synthesis was that of Albert Adelman, then president of the Milwaukee Jewish Federation. In three years of planning he secured Stone as architect and Helfaer as donor and, when the plan was known, he travelled to France to show Chagall and the weaver drawings of the atrium and samples of materials to be used and to convince the artist that the atrium space would be suitable for a tapestry. It would include a picture of Golda Meir, then premier of Israel, a former Milwaukeean, and a friend of Chagall. The tapestry was to "represent the unification of the Jewish people" and would show symbols for peace, unity, and understanding.

The atrium acts as a main lobby for receptions and as spill-out space where people mingle. Peter Capone, architect-in-charge from Stone's New York office, has noted, "The atrium was conceived as a unifying element, to express the feeling of oneness achieved by finally gathering all these organizations under one roof. It also offers a method of circulating throughout the building without deadly stretches of closed corridors. Its space and light help create an environment that people enjoy. The plants in the atrium offer a feeling of freshness and life, placid and serene in the middle of your tough Wisconsin winters."<sup>12</sup>

The three-story atrium has balconies on two sides which serve as corridors to the agencies's offices. The balconies were poured in place and cantilevered into the atrium. Offices opening off the balconies face Lake Michigan, for the site is on a bluff providing wide vistas of the lake. At the juncture of the L-shaped building is a glass facade 5/8-inch thick set in steel frames painted dark brown to match the dark brown anodized aluminum framing the fenestration. It has a coffered ceiling of square light wells. Except for twelve squares which are skylights, each well contains one large, clear glass bulb.

Along with tropical fig trees planted in four feet of soil, triangularly shaped benches of buff brick with oak tops and a reception desk of oak and brick enhance the lobby. Abundant banks of white anthermia add a solarium quality. Buff brick pavers form the floor while the balconies and stair rails are constructed of exposed concrete. The exterior is cream, buff brick. The street side is windowless except for the atrium. A grid of windows to the east and south has fins between the windows which point toward the lake.

Chagall's tapestry, mounted on a wooden frame held by brown twill binding, hangs on the atrium's north wall. Even on sunless days, with a strategically placed spotlight focused on the red "bird of joy," it provides an extraordinarily luminous impact upon the viewer.

At the dedication on April 30, 1973, Chagall's message described the tapestry's symbolism:

The image of the prophet tells of the history of the chosen people of God and in the pages are written the prophecies of Peace, of Wisdom, and of the comprehension between all the people of the earth for the future.

The red bird symbolizes the joy and the hope and he seems to sing the Song of Songs.

The color red of the bird makes an allusion to the long sufferings of the Jewish people in their travels through the centuries, of their sacrifices and of their innocence.

In the painting of the woman, I have thought of the women of the Bible, of Madame Golda Meir, and of all the valiant women of the earth. In depicting the other woman, my thoughts go to Madame Helfaer.

The blue represents the color of Hope and the new Israel.

The other bird, the blue, symbolizes the hope of life, of truth, and of good fortune for all of humanity.

The moon, in another era in my life, permitted us to dream of a better future.<sup>13</sup>

Mme. Prince spoke at this event:

I have lived after many months, day after day, with his thoughts in order for the tapestry to be truly the work of his heart and such as if his own hands had created it.

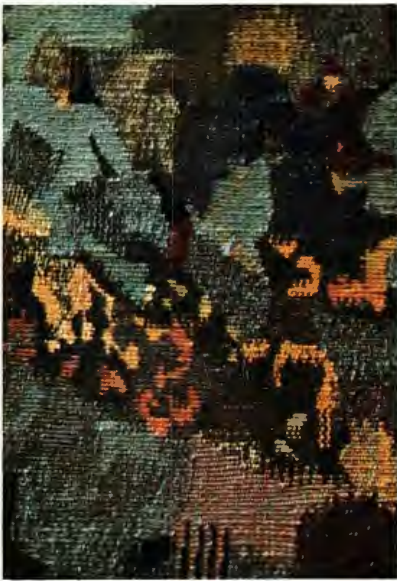
It represents a testimony of faith in humanity in spite of the horrors which have too often taken place. It is a work of love and hope such as is the life of Mrs. Golda Meir. It has been created especially for Milwaukee since Mr. and Mrs. Chagall share the thoughts of Mr. Helfaer. All that words could tell you the tapestry will express by itself and better than I could do it.<sup>14</sup>

In a moving moment of dedication, the Mezzuzah was affixed to the door post of the new building to fulfill the Biblical commandment, "Thou shalt write these words on the door posts of your house and upon your gates."<sup>15</sup>

In the tapestry, the gray images of the two women are placed beside the gorget of the large red bird. Here Golda Meir adds to the symbolism. Like Chagall, she came out of Russia and lived her share of happiness and anguish. Chagall's belief: "Art should speak to the soul rather than to the brain. Art and life itself seem to me like a boat upon the waters. To whom is it given, this gift of guiding this boat and how to sail it? I see the life of everyday people and things through a tear. I try to offer them, as I can, a plastic reflection."<sup>16</sup>



Figure 1. Symbolic of the Jewish faith, the only tapestry in the United States by Marc Chagall hangs in the Helfaer Community Center in Milwaukee, Wisconsin. The center was designed by Edward Durrell Stone. The large red bird symbolizes hope from the Biblical Song of Songs. One of the images of a woman beside the bird represents the life and inspiration of Golda Meir.



Figures 2 and 3. Details of the tapestry showing the modern solid weft weave which reflects the ancient Coptic technique.

Meir's belief: "It's no accident many accuse me of conducting public affairs with my heart instead of my head. I see no harm in it, on the contrary I've always felt sorry for people afraid of feeling, of sentimentality, of emotion, who conceal what they feel and are unable to weep with their whole heart. Because those who do not know how to weep with their whole heart, don't know how to laugh either."<sup>17</sup>

Born Golda Mabovitz in Kiev in 1898, she was brought to Milwaukee in 1906 where she had training and taught for an "after school" Labor-Zionist movement. She married Morris Meyerson in 1917 and emigrated to Palestine in 1921. From her past as ambassador to Moscow in Stalin's time, she rose to the premiership of Israel. To Henry Kissinger she "has always symbolized that the survival of a country is a serious business and that nothing is more important than the spirit of a country."<sup>18</sup>

When an interviewer called her a symbol, she replied, "Me, a symbol? What nonsense. Are you pulling my leg, by any chance? You have never met the great men who were truly the symbol of Israel: the men who founded Israel and shaped it. Of them all maybe Ben Gurion is left now, and I swear by my children and grandchildren I've never thought of myself in the same class as Ben Gurion." But, she added, "in my opinion, women can be good rulers, good leaders."<sup>19</sup>

The monumental figure in the tapestry is the prophet from the Old Testament. Chagall was not bound to precise religious meaning in his version of the Old Testament, and his view is not specifically theological. He interprets three groups which he has depicted in his prints, his illustrations, and his paintings. They were the great ancestors of the Jews who received the law, the makers of nationhood, and the visionary prophets of Israel. Meyer Schapiro writes that Chagall's vision of the Old Testament "traces the formation of a community and its highest values. . . and in the prophetic visions of the future, the setting of ideal goals. . . the prophet, the irrepressible man of moral courage, imbued with the most intense awareness of existence, speaks to the whole people."<sup>20</sup>

A strong Chasidic affinity is reflected in Chagall's imagery and composition. Chasidim considered reason, or reasonable conduct, as genuine obstacles to the knowledge of God, a notable example being the rabbi who became noticed by throwing somersaults in the marketplace. This image suggests Chagall's dynamic acrobatic figures which illustrate a primitive enthusiasm that leaves no part of a man's being insensible to the Chasidic power. The late Henry J. Seldis said, "His mythic dislocation of bodies and destruction of normal optical relationships, his shattering composition of space, time, and gravity, these elements of his art project the spirit of Chasidim where spontaneous emotion is as important as the law or the ritual of orthodox Judaism." Sir Herbert Read assessed the difference between experimentalists, like Picasso, and artists who, like Braque, find a personal equation and repeat it. He placed Chagall in the second category saying, "What is important is that an artist find a symbolic mode of expression." Chagall made that discovery.<sup>21</sup>

His art violates all canons of direct observation, yet he is called the most autobiographical of modern painters. Simone de Beauvoir found that the poetry of his form "grows richer and deeper in time. The great originality of Chagall's work lies in its autobiographical aspect . . . Deeply imbued with his own culture, he illustrates the Hebrew proverbs and he sets folklore down on

canvas. His landscapes, flowers, fabulous animals, mountebanks and lovers are seen as if in a dream; often there is an open window with the sleeper flying, taking to the air; although he does not show himself, the painter, nevertheless invites us to step into his dreams where the fishes are blue and the horses green, where fiddlers are perched upon the roof and where backgrounds lie stretched out in the sky. There is a sensual tenderness in this world of naive forms and shimmering colours."<sup>2 2</sup>

In 1947 Chagall wrote, "I have lived and worked in America during a time of universal tragedy for all men. I have not grown younger as the years went by. But I have drawn strength from the hospitable air of America. Yet my art retains its loyalties. For me a painting must have the due measure of painting as such. . . For me a picture is a surface covered with representations of things (objects, animals, human forms) in a certain way in which logic and illustration have no importance. Perhaps there is a mysterious fourth or fifth dimension—and not only of the eye—which intuitively gives birth to a scale of plastic and psychic contrasts, piercing the eye of the spectator with new and unaccustomed concepts. Neither so-called 'real colour' nor 'conventional colour' really colours the object. It is not what is called perspective which adds depth. Life itself creates contrasts without which art is unimaginable and incomplete."<sup>2 3</sup> In these words, uttered some thirty years ago, Chagall expressed a credo for his tapestry.

Mme. Prince calls him, "Unique for our century. He is the greatest painter of Love and Life which we have. Love of Animals, the Sun, the Flowers, Men, Women, Color, Spring. . . always Love. He understands the Sadness and hard times in Life. . . but he sees beyond it. . . to the Beauty."

Chagall has said that he dwells somewhere between sky and earth, which may be some airborne field of flowers. There is an ascending scattering of multi-colored flowers below the red bird in the tapestry. Flowers move in and out of his paintings like emblems of joy. He keeps fresh flowers in the atelier to consult as a color guide and bids his wife to remove them when they fade. During his visit to Chicago in 1974 preceding the unveiling of the Four Seasons mosaic for the First National Bank plaza, he painted in ten days fifteen watercolors from the many bouquets sent to him by admirers. "The end of life is a bouquet," he has said, for the act of making a bouquet ensures its decay and death. Since he cannot make the flowers, he continues nature into art and paints the perishable produce of his love."<sup>2 4</sup>

When then President Valéry Giscard D'Estaing decorated Chagall with the French cross of the Legion of Honor, he said it was "in the name of France, of flowers, animals and the three muses that have been your inspirations: work, the Bible, and liberty." These inspirations have been woven into the Milwaukee tapestry.

<sup>1</sup> Alan Artner, "Marc Chagall Talks About Life and Love," *Chicago Tribune*, September 25, 1974.

<sup>2</sup> James Auer, "Chagall Artistry to be Unveiled," *Milwaukee Journal*, April 29, 1973, part 5, p. 5.

<sup>3</sup> Phyllis Schnur, "Weaver Transposes Vision to Art Work," *Wisconsin Jewish Chronicle*, May 4, 1973, p. 1.

<sup>4</sup> James Auer, "Tapestry Shows Chagall Genius," *Milwaukee Journal*, May 4, 1973, part 5, p. 2.

<sup>5</sup> John Beckwith, "Coptic Textiles," *CIBA Review* 12, no. 133 (August 1959): 3.

<sup>6</sup> Mirritt Boufros Ghali, *Coptic Art: A Brief Introduction* (Cairo: Society for Coptic Archeology, June 1966).

<sup>7</sup> William S. Lieberman, "Modern French Tapestries," *Metropolitan Museum of Art Bulletin* 6, no. 5 (January 1948): 142-49.

<sup>8</sup> Simone de Beauvoir, *All Said and Done* (New York: G. P. Putnam's Sons, 1974), p. 204.

<sup>9</sup> Roy McMullen, *The World of Marc Chagall* (New York: Doubleday, 1968), pp. 124-27.

<sup>10</sup> Beverly Johnson, "Tapestries From France," *Los Angeles Times*, August 31, 1961, Home Section, p. 1.

<sup>11</sup> Lois Hagen, "Jewish Agencies Under One Roof," *Milwaukee Journal*, May 3, 1973, part 7, p. 2.

<sup>12</sup> Ello Brink, "Unity, Dignity on Prospect," *Milwaukee Journal*, May 18, 1975, part 7, p. 1.

<sup>13</sup> Marc Chagall, "Statement," permission to use granted by Lawrence Tarnoff, Milwaukee Jewish Federation. April 19, 1973.

<sup>14</sup> Yvette Cauquille-Prince, "Dedication Message," permission to use granted by Lawrence Tarnoff, Milwaukee Jewish Federation. April 19, 1973.

<sup>15</sup> Phyllis Schnur, "Building Dedicated, Tapestry Unveiled," *Wisconsin Jewish Chronicle*, May 4, 1973, p. 3.

<sup>16</sup> Paul Steiner, "Chagall's Views on Art, Life," *Des Moines Register*, May 15, 1965, p. 6.

<sup>17</sup> Oriana Fallaci, "Golda Meir Talks with Oriana Fallaci," *Ms. Magazine*, April 1973, pp. 75-104.

<sup>18</sup> Anonymous, "Golda Meir," *Milwaukee Journal*, Dec. 20, 1975, part 1, p. 1.

<sup>19</sup> Fallaci, p. 104.



<sup>20</sup>Meyer Schapiro, "Chagall's Vision of the Old Testament," *Harper's Bazaar*, November 1956, pp. 137-82.

<sup>21</sup>Henry J. Seldis, "The Anatomy of Marc Chagall's Personal Idiom," *Los Angeles Times*, September 17, 1972.

<sup>22</sup>De Beauvoir, p. 204.

<sup>23</sup>Michael Ayrton, *Notes by the Artist: Chagall* (London: Faber and Faber, Ltd., 1948), p. 20.

<sup>24</sup>Jon Borgzinner and Jonathan Randal, "Chagall Self-Portrait," *Time*, July 30, 1965, p. 50.

*EYSENHARDTIA* (LEGUMINOSAE: PAPILIONOIDEAE)<sup>1</sup>

James M. Lang and Duane Isely<sup>2</sup>

**ABSTRACT.** This is a taxonomic-geographic summary of the largely Mexican leguminous genus, *Eysenhardtia*, 11 species. Data include those of gross morphology, distribution, ecology, and calcium oxalate crystal distribution and to a lesser degree cross-compatibility relationships, leaflets venation, and stomatal types. Conclusions derive from a comparison of empirical conjectures and computer analyses. One new variety, *Eysenhardtia orthocarpa* var *tenuifolia*, is described.

Additional index words: Oxalate crystals in plants, *Eysenhardtia orthocarpa* var *tenuifolia* var nov.

This review of *Eysenhardtia* is summarized from the doctorate dissertation of the senior author (Lang, 1972). The original manuscript includes also an extensive discussion of the tribal relationships of the Amorphaeae (as Daleceae) and of the affiliations of its component genera. Primary data are those of gross morphology and calcium oxalate crystal distribution. The latter, determined from specimens of about 130 species, include presence vs absence and location (variously leaf mesophyll or epidermis, or calyces) of crystals. Lang largely agrees with Barneby (1977) concerning the relationships of the genera within the Amorphaeae but not with the latter's postulate that a close relationship between the Amorphaeae and Psoraleae is unlikely. Those interested in Lang's opinions in these matters must turn to the manuscript (Lang, 1972).

*EYSENHARDTIA*

*Eysenhardtia* is a small, primarily Mexican xerophytic genus of shrubs or small trees of the tribe Amorphaeae (Polhill and Raven, 1981). It and the related monotypic *Apoplanesia* (southern Mexico to Venezuela) are uniquely characterized by a slightly irregular but nonpapilionoid corolla. *Apoplanesia* differs from *Eysenhardtia* in calyx lobes several times as long as the tube. The other immediate relatives of *Eysenhardtia* are *Parryella* Gray, *Errazurizia* Phil., and *Amorpha* L. (Lang, 1972, Barneby, 1977), all of which are characterized by striking modifications of the usual papilionoid corolla.

Classically, *Eysenhardtia* has been but vaguely known. Staph (1909), as recently as the present century, following a summary of the scant information, concluded that there were but "three well distinguishable species." *Eysenhardtia*, however, was evidently the source of the once famed and

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mysterious Mexican *Lignum nephriticum*, a wood that, particularly in seventeenth-century literature, was alleged to have remarkable medical qualities. Though the wood is white, a water infusion from it, under certain illumination conditions, would turn blue (a fluorescence phenomenon). The history of *Lignum nephriticum* and its identification with *E. polystachya* have been detailed successively by Staph (1909) and Safford (1915a, 1915b).

Prior summaries of *Eysenhardtia*, those of Pennell (1919) and Standley (1922), were based primarily on resources then available in the herbaria of the New York Botanical Garden and the United States National Museum, respectively. Data for the present treatment derive from 18 herbaria and from study of gross morphology, leaflet venation, stomatal types, and crystal distribution. Chromosome counts were made on three species. Some field-knowledge was obtained during one season's work in Mexico. Several species were grown in the greenhouse and crosses made between them. Both empirical evaluations and cluster analysis computations were used in formulating taxonomic concepts.

Lang's manuscript also describes supporting methodology and provides a summary of the taxonomic history of *Eysenhardtia*, illustrations, photographs of type specimens, and an exsiccatae list. The economics of publication necessitate reference to that manuscript for those details.

*Eysenhardtia* is evidently a genus in the early stages of evolutionary divergence and hence taxonomically "difficult." Morphological differentiation of the taxa is minor and essentially all of them merge in areas of sympatry. Greenhouse studies of *E. polystachya*, *E. texana* and *E. spinosa*, demonstrating much more successful seed-set from cross- than from self-pollination, imply that outcrossing probably predominates in nature. Cross-pollinations between these species were essentially as successful as those within species; i.e., all were highly interfertile. This suggests the probability of continuing genetic contact between species in nature where their ranges overlap and provides a plausible explanation of intermediacy observed among specimens from such areas.

On the basis of both intuitive taxonomy and cluster analyses, which are largely confirmatory, we believe the taxa described, though peripherally confluent, have objective reality. Their taxonomic status, however, is arguable. Considering that biological knowledge of *Eysenhardtia* is as yet relatively limited, we have followed a conservative course and classified most of the taxa as species. The junior author, however, suspects that further studies might materially reduce the number of considered species.

#### Chromosome Counts (meiotic determinations)

*Eysenhardtia polystachya* n = 10. Voucher: Lang 4915 (ISC) derived from seed from Ripley & Barneby 14,870, Mexico, Mexico.

*E. spinosa* n = 10. Voucher: Lang 4914 (ISC) derived from Ripley & Barneby 13,863, Chihuahua, Mexico.

*E. texana* n = 10. Voucher: Lang 4916 from seed collected at Leakey, Texas.

*Parryella filifolia* n = 10. Voucher: Lang 4917 derived from ARIZ specimen (seed voucher number lost).

The above, first counts for all but *Eysenhardtia texana*, indicate that *Eysenhardtia* is probably consistent with the other members of the *Amorpheae* except *Dalea* in a base number  $\times = 10$ . The only prior count for *Eysenhardtia* is that of Turner (1959), *E. texana*,  $2n = 20$ . The occurrence of polyploidy within *Eysenhardtia* remains to be studied.

#### Herbarium Materials

Specimens used in this study were borrowed from the following herbaria: ARIZ, CAS, DS, F, GH, ISC, LL, MEXU, MICH, MO, NY, P, RSA, SD, SMU, UC, US, and TEX (abbreviations those of Holmgren and Keuken, 1947).

#### Nomenclature

Names deriving from one type are listed in a single paragraph. All protologues were seen in the original. Types of nearly all names were available. Affirmation is indicated by the conventional exclamation mark following the herbarium citations of holotypes and isotypes.

#### Manuscript Shorthand

##### Length and Width

Dimensions of length alone are not qualified as to direction: 2 cm = 2 cm long. Where both length and width are specified,  $2 \times 1$  cm = 2 cm long and 1 cm wide. When only width is stated, it is identified as such.

##### Parenthetical Statements in Descriptions Marked by a Hyphen

These indicate exceptions in size or condition. Examples: *Leaves (4-) (6-10) (-12)* means the leaves are usually 6-10 cm long, but occasionally as short as 4 cm and sometimes as long as 12 cm. *Leaves pubescent (-glabrate)*. The leaves are usually pubescent but occasionally glabrate.

#### EYSENHARDTIA H.B.K.

*Eysenhardtia* H.B.K., Nova Gen. Sp. 6: ed. fol. 382, ed. quar.

489. Sept. 1824. nom. cons. Type *Eysenhardtia amorphoides* H.B.K. = *E. polystacha* (Ort.) Sarg.

*Viborqua* Ort., Nov. Rar. Pl. Hort. Matr. Descr. 5: 66. 1798.

nom. rej.; *Varennea* DC., Prod. 2: 522. 1825; *Wiborgia*

Kuntze, Rev. Gen. Pl. 1: 213. 1891.

Shrubs or much branched, small trees to 20 (-25) m. Young growth cinereous to canescent with usually incurved or appressed bicellular hairs. Leaves alternate, imparipinnate; leaflets petioluled, ca. 11-61, oblong to elliptic-oval, permanently pubescent or not, glandular-punctate. Stipules 1-5 mm, subulate, pubescent. Stipels present (-absent) bristle-like to subulate, pubescent. Inflorescences racemose or spiciform, 3-10 cm, usually arranged in cymose clusters. Bracts lanceolate (-ovate-lanceolate), 1-2 (-4) mm, pubescent,

deciduous before anthesis or persistent. Pedicels .5-1 (-2) mm. Calyx ca. 2.5-5 mm, pubescent, with epidermal crystals; tube oblique, persistent, entire or ventrally (above standard) incised, commonly split in fruit; teeth deltoid, ca. 1 mm or less, unequal, ventral longest. Corolla slightly irregular but not papilionoid; petals 5-10 mm, free, inserted on the hypanthium, white (-rose-tinted), oblanceolate or obovate, proximally tapering; standard truncate or notched, broader than the other petals. Stamens ten, diadelphous; ventral stamen longest, the remaining nine united about one-half their length into an apically oblique tube, of alternating short and long pairs diminishing in length towards the free stamen. Ovary sessile, glabrous; ovules 2; style slender, pubescent, abruptly up-curved near the tip, with or without a conspicuous gland at the bend; stigma large, capitate. Legumes ascending-spreading or deflexed, indehiscent, oval to oblong or oblanceolate-oblong, laterally compressed, 5-20 mm, glabrous. Seed solitary, pendulous, usually not filling fruit cavity, the hilum near the distal end.

Southwestern United States, Mexico, south to Guatemala and El Salvador. 11 species. Chromosome base number  $\times = 10$ .

#### KEY TO SPECIES OF *EYSENHARDTIA*

1. Style bend eglandular; leaflets 25 (-29) or fewer.
  2. Leaflets 11 or fewer,  $> 7.5$  mm, slightly oblique; Baja California. *E. peninsularis*
  2. Leaflets 13 or more, or  $< 7$  mm long, not oblique; not of Baja California.
    3. Calyx split to the base in fruit; legume length  $< 3 \times$  width.
      4. Legumes with conspicuous longitudinal veins; leaflets 17 or fewer. *E. spinosa*
      4. Legumes without conspicuous veins; leaflets 19 or more. *E. schizocalyx*
    3. Calyx not split to the base in fruit; legume length  $3-4 \times$  width.
      5. Leaflets 13 or fewer, their glands limited to a row on each side of the midrib; leaves  $< 10$  mm; Chihuahua and San Luis Potosi. *E. parvifolia*
      5. Leaflets more than 15, their glands scattered over entire surface; leaves  $> 11$  mm; Durango, east to southern Tamaulipas, south to Oaxaca. *E. polystachya*
  1. Style bend glandular; leaflets 25 or more (-fewer in depauperate specimens).
    6. Leaflet glands of two sizes, the larger along the main vein and leaflet margins; legumes ascending-spreading; northeastern Mexico and Texas. *E. texana*
    6. Leaflet glands various in size or the larger randomly distributed; legumes variously positioned, ascending to reflexed-spreading.
      7. Flowers and legumes ascending-spreading.
        8. Leaflets green on both sides,  $< 13.5$  mm with large (.25-.4 mm) glands; epidermal cells of lower surface not mammillate. *E. punctata*
        8. Leaflets pale beneath,  $> 12.5$  mm, with small (.15-.25 mm) glands; epidermal cells of lower surface mammillate.

- 9. Legumes  $> 15$  mm, splitting the subtending calyx one-fourth of length or more; central Chiapas southeast to El Salvador. *E. adenostylis*
- 9. Legumes  $< 14$  mm; calyx entire or split less than one-fourth of length; central Oaxaca northwest to Sinalo. *E. platycarpa*
- 7. Flowers deflexed after anthesis and legumes reflexed-spreading.
  - 10. Calyx one-half or  $>$  length of the corolla. *E. subcoriacea*
  - 10. Calyx  $<$  one-half the length of the corolla.
    - 11. Stipels  $>$  petiolules. *E. polystachya*
    - 11. Stipels = or  $<$  than petiolules. *E. orthocarpa*

# *EYSENHARDTIA ADENOSTYLIS* Baillon

*E. adenostylis* Baill., Adansonia 9: 239. 1870. Type: Guatemala: 1846, *Savage s.n.* Holotype P!

Tree, 2-18 (-24)m. Stems gray-brown. Pubescence of strigulose or puberulent hairs. Leaves 9-19 cm; petiolules 1-1.9 mm; leaflets 35-53, oblong, 15-25 mm, firm, dull-green above, finely puberulent, glaucous-oblong, 15-25 mm, firm, dull-green above, finely puberulent, glaucous-whitened with mam-millate cells, finely puberulent and minutely punctate beneath. Stipules 2-5 mm, grayish brown; stipels subulate, .6-1.5 mm, persistent. Racemes 4-12 cm in compact clusters; bracts deciduous. Pedicels 1-1.8 mm. Calyx tube 2.5-4 mm, obscurely glandular-dotted, canescent-puberulent, split on the dorsal side; teeth .2-5 mm, acute. Petals 6-9 mm, firm. Style 3-4 mm, the subterminal gland present, large and conspicuous. Legumes ascending-spreading, 14-21  $\times$  4-5 mm, thin, brown, distally punctate with small glands, usually straight. Seed 7 mm, oblanceolate, flat, smooth, olive-brown, filling one-third to two-fifths of the fruit.

Southern Mexico (Chiapas), Guatemala and western El Salvador. Moist slopes or near creeks or drainageways; oak-pine zone. Elevation (800-) 1,000-2,300 (-2,700)m. Flowering: late July, early January. Fruiting: October-February.

*Eysenhardtia adenostylis* resembles *E. platycarpa* of west-central Mexico and the two are presumably closely related. Both have large, compact inflorescences and large, ascending-spreading, usually straight fruits. The mam-millate epidermal cells cause the lower surface of the leaflets to appear lighter than the upper.

This is the only *Eysenhardtia* of its region; it is disjunct from any others by approximately 330 km.

# *EYSENHARDTIA ORTHOCARPA* (A. Gray) Watson

A shrub or small tree, 3-5 m. Stems grayish-brown. Pubescence of incurved hairs. Leaves 2-14 cm; petiolules .3-1.1 mm; leaflets 17-43, oblong, 5-20 mm, membranous, pubescent on both surfaces, dull-green above, paler and punctate beneath. Stipules 1.6-4.5 mm, stipels bristle-like, from a broad base, .2-.9 mm, soon deciduous. Racemes 5-10 cm; bracts deciduous. Pedicels 1 mm. Calyx-tube 2-3.5 mm, distinctly glandular-dotted, finely pubescent or glabrescent, sometimes split slightly on the dorsal side; teeth .3-.8 mm, acute, pubescent.

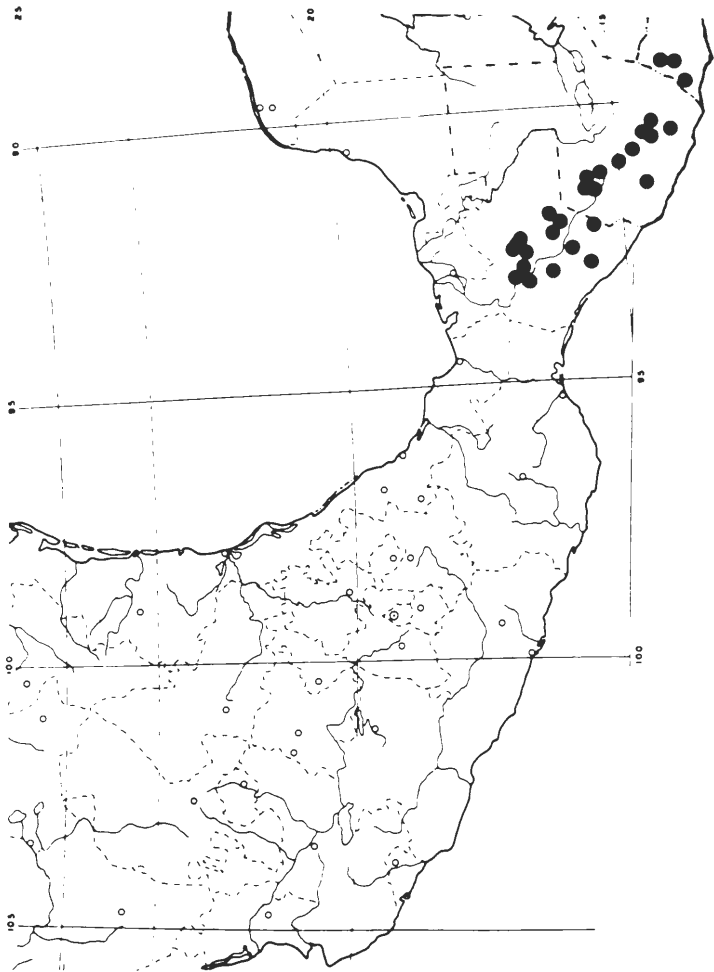


Figure 1. *Eysenbardtia adenostylis*.

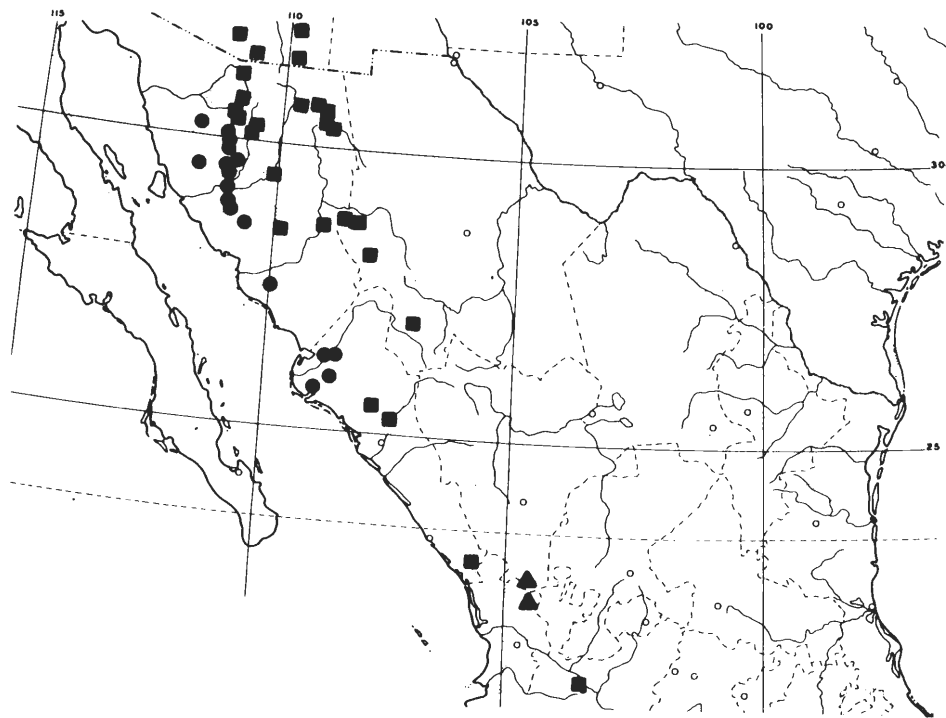


Figure 2. *Eysenhardtia orthocarpa* var. *orthocarpa* □; *E. orthocarpa* var. *tenuifolia* ○; *E. orthocarpa* × *platycarpa* (putative) Δ.



Petals 6-10 mm, membranous. Style 4-5 mm, with conspicuous subterminal gland. Legumes typically reflexed-spreading at maturity, 10-16 × 2.5-4.2 mm, thin, greenish-brown, glabrous, straight or slightly upcurved at the apex, inconspicuously punctate distally with small glands. Seed filling one-half of the fruit, oblanceolate, 4.5-5.5 mm, flat, smooth, olive-brown.

United States: southeast Arizona. Mexico: Chihuahua, Sonora, Sinaloa, Nayarit, and Jalisco. Rocky slopes and washes in pine-oak forest, thorn forest, and desert scrub. (100-) 300-1,600 (-2,000) m. Flowering: March-September. Fruiting: June-September.

*Eysenhardtia orthocarpa* includes two geographic-ecological phases slightly morphologically differentiated. Empirical differentiation is confirmed by computer interpretation of data.

#### Key to Varieties of *EYSENHARDTIA ORTHOCARPA*

1. Leaflets minutely pubescent to canescent; plants of middle elevations, 1,000-2,000 m, pine-oak forest; range as given for species, Arizona to Jalisco. *E. orthocarpa* var. *orthocarpa*
1. Leaflets glabrous to glabrescent; plants of lower elevations, 100-1,200 m, thorn forest and desert scrub; Sonoran Desert, west of above in Sonora and Sinaloa, and at lower elevations. *E. orthocarpa* var. *tenuifolia*

#### Var. *ORTHOCARPA*

*Eysenhardtia orthocarpa* (Gray) Wats., Proc. Amer. Acad. Arts Sci. 17: 339. 1882. *Eysenhardtia amorphoides* H.B.K. var. *orthocarpa* Gray, *Plantae Wrightianae*, Smiths. Contr. Knowl. 5 (art. 6): 37. 1853. *Viborqua orthocarpa* (Gray) Cockerell, Bull. Amer. Mus. Nat. Hist. 24: 97. 1908. Type: Mexico: N. Mex. [Sonora], 1851. Wright 980. Holotype GH! Isotypes MO! NY!

*Eysenhardtia reticulata* Pennell, N. Amer. Fl. 24: 36. 1919. Type: Mexico, Jalisco: Barranca of Guadalajara, 30 July 1902. Pringle 9752. Holotype NY! Isotypes F! MEXU! MO!

Range and habitat as given in key.

Variety *orthocarpa* usually has larger leaves, leaflets, and corollas and longer stipules than var *tenuifolia*. The distinctive, large, calyx glands are more common.

Although the type of *Eysenhardtia reticulata* is *E. orthocarpa* var. *orthocarpa*, some specimens annotated by Pennell as *E. reticulata* also include *E. polystachya*, *E. orthocarpa* var. *tenuifolia*, and intermediates between *E. orthocarpa* and *E. platycarpa*.

#### *EYSENHARDTIA ORTHOCARPA* Var. *TENUIFOLIA* Lang, Var. nov.

Frutex ramosus 3 m usque altus; folia 12 cm usque longa, foliolis glabris tenuibus 14 mm usque longis; stipulae liberae 3.2 mm usque longae; stipellae setaceae brunneo-rubrae 0.6 mm usque longae; calyx glandulis minimis instructus.

Type: Mexico, Sonora: erect shrub 2-4 m high, talus slope of a sandstone hill, 20 miles south of Hermosillo on road to Guaymas, 1 Sept. 1941, *Wiggins & Rollins 213*. Holotype ARIZ! Isotypes MICH, NY, UC, US!

Shrub 1.5-3 m high. Leaves 2-12 cm. Leaflets 15-37, oblong, 5-14 mm, glabrescent at maturity, minutely punctate beneath. Stipules 1.6-3.2 mm. Calyx tube 2.5-3.5 mm, scantily or evidently glandular-dotted, glabrescent. Petals 6-8 (-9) mm.

Range and habit as given in key.

Variety *tenuifolia* differs from var. *orthocarpa* in its usually smaller leaves, leaflets and flowers, shorter and subulate stipules, and less abundantly glandular calyx. It seems to be a desert adaptation of the more widely distributed and diverse var. *orthocarpa* and is largely confined to the "Arbosuf-frutescent Desert" of Shreve and Wiggins (1964).

#### EYSENHARDTIA PARVIFOLIA Brandegee

*Eysenhardtia parvifolia* Brandg., Univ. Calif. Publ. Bot. IV. 4:

179. 1911. Type: Mexico, Coahuila: Sierra de Parras, Oct.

1910. *Purpus 5074*. Holotype UC! Isotypes F! MO! NY!

Intricately branched shrubs. Stems gray to black. Leaves .5-1 cm, spreading; leaflets 9-13, elliptic-oval, 2-2.5 mm, fleshy, green-glabrate to pubescent above; paler, glabrate, glandular beneath, with glands in a single line along each side of the main vein. Stipules .5-1.5 mm, filiform; stipels absent or minute and early deciduous. Racemes .5-1 cm; bracts 1-2 mm, persistent. Calyx-tube 2.5-3 mm, dotted with large glands, canescent-puberulent, split slightly on the dorsal side; teeth .3-.5 mm. Petals 5-6 mm, membranous. Style 3-4 mm, pubescent with long hairs, eglandular. Legumes ascending, 7-10 × 1.7-2 mm, brown, punctate with large glands. Seed filling the entire fruit.

Mexico: Coahuila and San Luis Potosi. Steep limestone slopes and canyon sides in desert scrub. Elevation ± 1,800 m. Flowering: July-December. Fruiting: August-December.

This species, presently known from only five localities, is clearly marked by several characters: the small leaves with few leaflets, the absence of stipels, the distribution of foliar glands, and the uniquely large glands of the fruit. Its relationships are uncertain. One specimen is a suspected hybrid between *E. parvifolia* and *E. punctata*.

#### EYSENHARDTIA PENINSULARIS Brandegee

*Eysenhardtia peninsularis* Brandg., Univ. Calif. Publ. Bot. IV. 4:

180. 1911. Type: Mexico, Baja California: Paraiso, May

1889. *Brandegee s.n.* Holotype UC! Isotype NY!

An intricately branched shrub. Stems gray. Pubescence incurved or appressed. Leaves 1.5-2 cm, leaflets 9-13, oblong, oblique at the base, 5-7 mm, firm, puberulent or glabrate on both surfaces, dull-green above, punctate mostly along margins. Stipules 2-3 mm; stipels subulate, .3-.5 mm, ± the petiolules, persistent. Racemes 2-5 cm; bracts persistent. Calyx 2.5-3 mm,

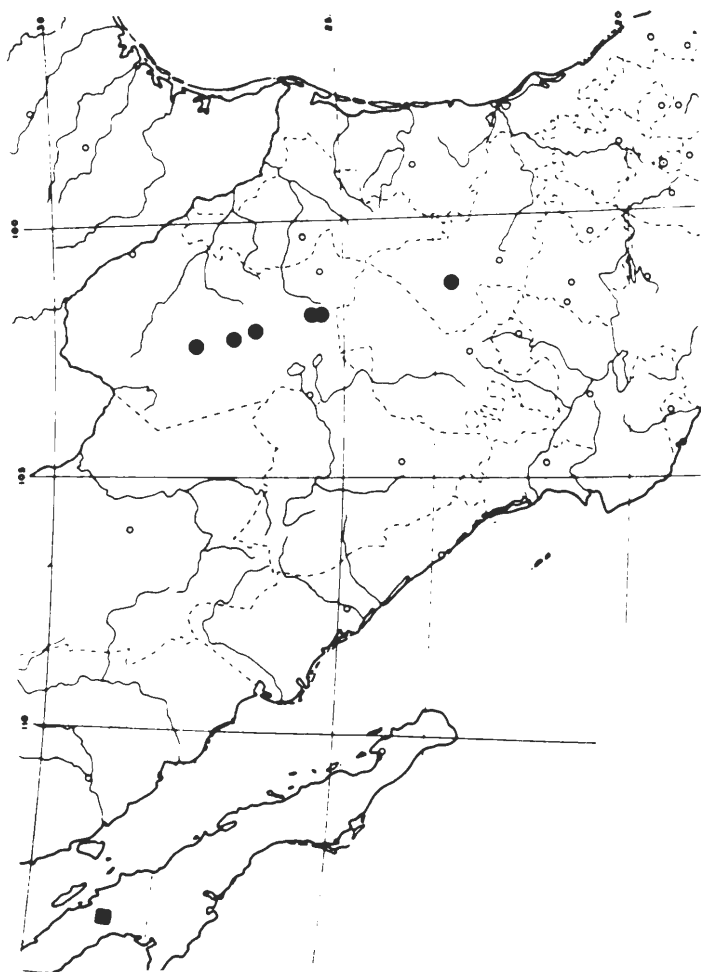


Figure 3. *Eysenbardia parvifolia* ○; *E. peninsularis* □.

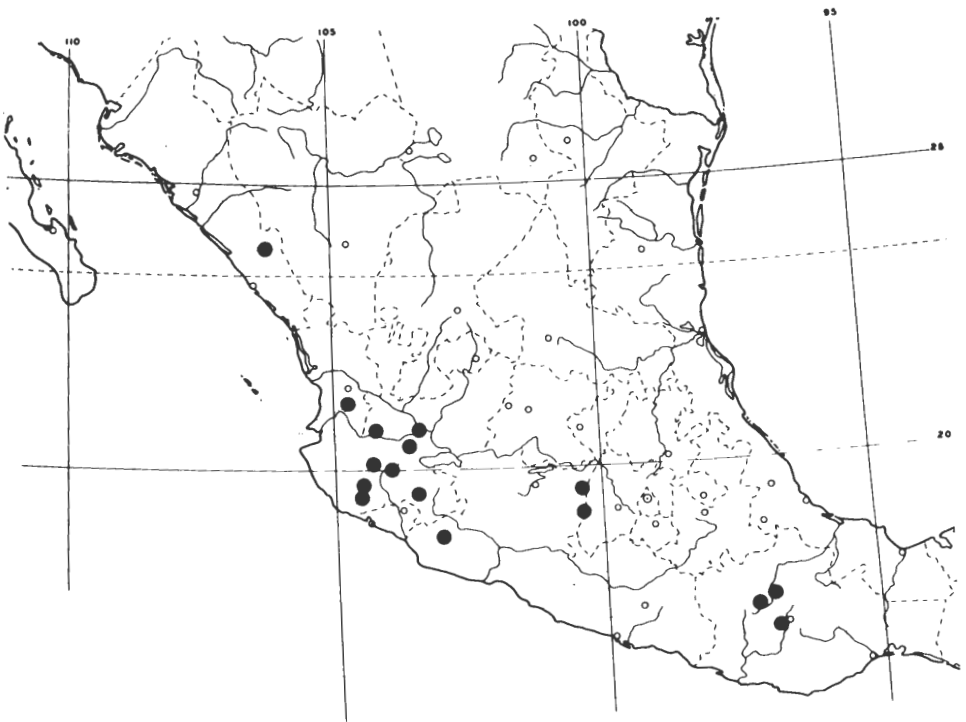


Figure 4. *Eysenhardtia platycarpa*. The three dots in Oaxaca represent *E. cobriformis* of Pennell (1919).

glandular-dotted, canescent, ridged, split on the dorsal side; teeth subequal, .8-.9 mm. Petals 5-6 mm, membranous. Style eglandular. Fruit not seen.

Known only from type collection, Paraiso, Baja California. Flowering: May.

*Eysenhardtia peninsularis* resembles *E. spinosa* in most qualitative characters. Apart from its geographical isolation from that species, the single specimen has fewer, slightly oblique leaflets, and the glands are more concentrated toward the leaflet margins than in *E. spinosa*. Probably *E. peninsularis* constitutes a relic population that should be reduced to varietal status under *E. spinosa*. Its existence suggests that *E. spinosa* (or its progenitors) once had a wider distribution than at present.

Despite considerable botanical activity in Baja California during the last twenty years, *Eysenhardtia peninsularis* has not been rediscovered. Evidently it is very local or possibly extinct.

### *EYSENHARDTIA PLATYCARPA* Pennell & Safford

*Eysenhardtia platycarpa* Pennell & Safford, N. Amer. Fl. 24: 37. 1919. Type: Mexico, Jalisco: Barranca of Guadalajara. 24 Oct. 1863. *Pringle* 8672. Holotype NY! Isotypes CAS! F! MO! UC!

*Eysenhardtia cobriformis* Pennell, N. Amer. Fl. 24: 36. 1919. Type: Mexico: Monte Albán near Oaxaca City, Oct. 1894. *C. L. Smith* 337. Lectotype NY! (Specimen at base of sheet; see discussion.) Isotypes F! MEXU! MO! NY! UC!

A shrub or tree, 3-6 (-10) m. Stems grayish-brown. Pubescence of appressed hairs. Leaves 9-15 cm; petiolules 1-1.6 mm; leaflets 41-51, oblong, 12-19 mm, firm, minutely puberulent on both surfaces, dull-green above; much paler (cellular-mammillate) beneath and minutely punctate. Stipules 2.5-4.2 mm. Stipels subulate, .6-1.4 mm, persistent. Racemes 4-12 cm; bracts deducous. Pedicels 1 mm. Calyx tube 2.2-2.7 mm, obscurely glandular-dotted, canescent-puberulent, split slightly on the upper side; teeth .2-.4 mm, acute to obtuse. Petals 5.5-7 mm, firm. Style 3-4 mm, with large subapical gland. Legumes ascending-spreading, 13-14 × 4-4.5 mm, straight, thin, greenish-brown, punctate distally with medium to large glands. Seed filling one-third to two-fifths of the fruit.

Sinaloa (southern part), Jalisco, Michoacan, Guerrero, and Oaxaca. Stream valleys or steep rocky slopes in the pine-oak zone. 1,300-2,000 (-2,300) m. Flowering: July-December. Fruiting: October-December.

*Eysenhardtia platycarpa* is approximately a Mexican analogue of the isolated *E. adenostylis*; both have large leaves with numerous leaflets that are pale beneath from mammillate epidermal cells. Also both have ample, compact inflorescences with large, ascending-spreading, usually straight fruits. Beyond its geographic isolation, *E. platycarpa* has somewhat smaller leaflets and fruits, and its mature calyx usually fails to split. Of the two, the morphological variability of *E. platycarpa* is somewhat the greater, possibly a consequence of genetic interchange with contiguous species. *E. punctata*, the other species with large leaves and ascending fruits, has a more open inflorescence and smaller leaflets which are not bicolored.

Pennell's simultaneously published *E. cobriformis* (loc. cit.) differs from *E. platycarpa* as to description in having smaller leaves with fewer leaflets, smaller glands on the pods, and misleadingly reflexed-spreading pods. Three specimens from Oaxaca referred to *Eysenhardtia cobriformis* by Pennell are disjunct from the main range of the species and perhaps differ slightly.

The holotype sheet (NY) of *E. cobriformis* contains two specimens evidently from different plants. The young fruits on the specimen at the bottom of the sheet are spreading-ascending (the posture of the fruits is more distinct on a more mature inflorescence of the MO isotype). Contrariwise, the fruits of the specimen at the top of the sheet are pendent. We regard the first-named specimen as *E. platycarpa*, the second probably as a hybrid between *E. platycarpa* and *E. polystachya*. Were the latter specimen considered the type to accord with Pennell's protologue statement "pods . . . at maturity reflexed-spreading," *E. cobriformis*, rather than being a synonym of *E. platycarpa*, would represent a hypothetical hybrid category. In view of the character of the isotypes and the fact that two other specimens annotated by Pennell are *E. platycarpa* of our interpretation, we have maintained it as a synonym of that species. In essence then, we have designated the lower specimen of the type sheet as lectotype.

#### EYSENHARDTIA POLYSTACHYA (Ortega) Sargent

*Eysenhardtia polystachya* (Ort.) Sarg., Silva N. Amer. 3: 29.

1891. *Viborquia polystachya* Ort., Nov. Rar. Pl. Hort. Matr. Descr. 5: 66, tab. 9. 1798. *Varennea polystachya* (Ort.) DC., Prod. 2: 522. 1825. *Wiborgia polystachya* (Ort.) Kuntze, Rev. Gen. Pl. 1: 213. 1891. Type: *non vidi*. Holotype presumably MA.

*E. amorphoides* H.B.K., Nov. Gen. Sp. Plantarum ed. quar. 6: 491, tab. 592. 1824. Type: Mexico: San Augustin. *Humbolt*. Holotype P-HBK (Microform. IDC. Herb H.B.K. (6209). Lab. de Phan. Paris. V. no. 165!).

*Dalea fruticosa* G. Don, Gen. Hist. Pl. 2: 226. 1832. (fide Barneby, 1977, p. 587).

*Psoralea fruticosa* Sessé & Mociño, Pl. Nov. Hisp. 121. 1889. (fide Barneby, 1977, p. 588).

A shrub or small tree 1-4 (-6) m. Stem grayish brown. Pubescence of ascending or incurved hairs. Leaves 2-11 cm; petiolules .3-1.2 mm; leaflets 29-61, oblong, 4-14 mm, membranous, pubescent on both surfaces, dull-green above, paler and punctate beneath with minute brown glands. Stipules 1.2-5.2 mm, stipels subulate, .3-1.4 mm, subequal or > petiolules, persistent. Racemens 4-14 cm; bracts 2-4 mm, deciduous. Pedicels .5-1 mm. Calyx tube 2-4.2 mm, glandular-dotted, slightly split on the dorsal side; teeth .2-.6 mm, acute. Petals 4-9 mm, membranous. Style 3-4 mm, subterminal gland small (-large) or absent. Legumes reflexed-spreading at maturity, straight or slightly upcurved at the apex, thin, pale brown (with or without reddish-brown blotches), inconspicuously punctate distally with minute glands. Seed filling one-half of the length of the pod, obovoid-oblanceolate, 4.5-5 mm, light brown.

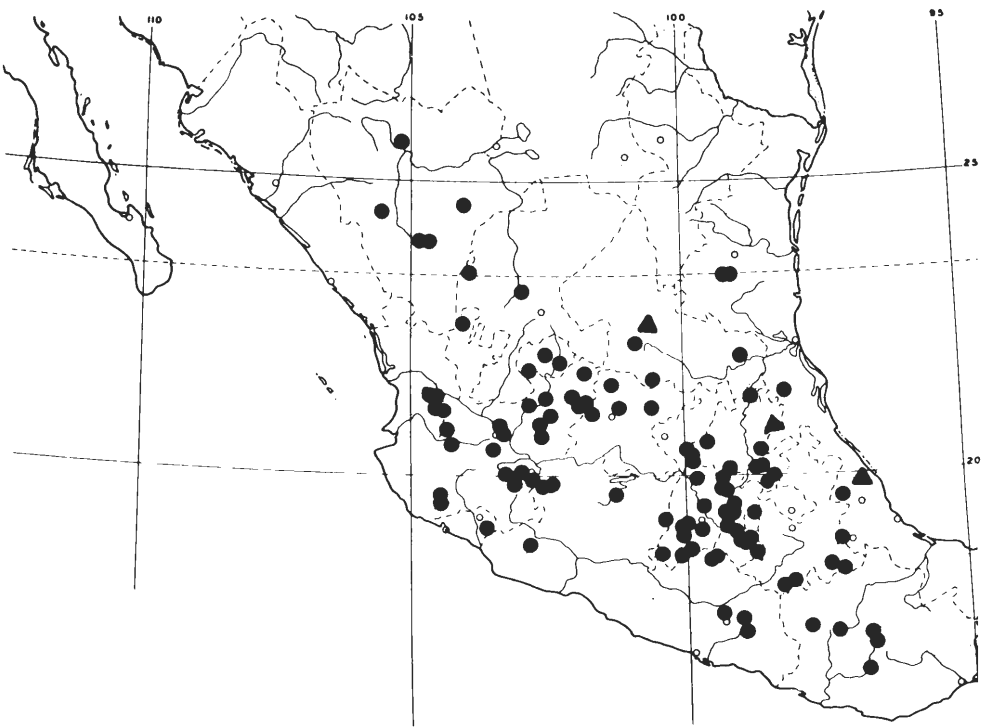


Figure 5. *Eysenhardtia polystachya* ○; *E. polystachya* × *E. texana* (putative) ▲.

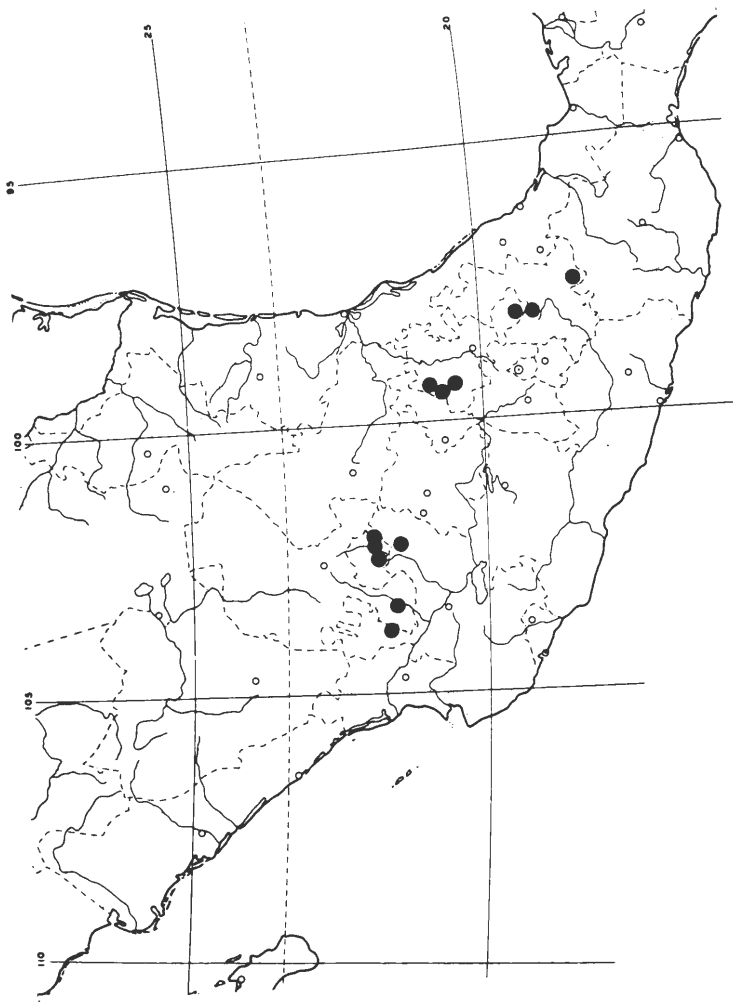


Figure 6. *Eysenhardtia punctata*.



Mexico: Durango east to southern Tamaulipas, south to Oaxaca. Open sparsely-forested slopes and heavily grazed or burnt over areas in pine-oak forest, chaparral, and mesquite-grassland. (1,000-) 2,000-2,600 (-3,200) m. Flowering: June-October. Fruiting: August-January.

Material that we have referred to *Eysenhardtia polystachya* is diverse. The stipels that exceed the petiolules furnish essentially the only constant reference character. This feature, however, is possessed by plants that usually have numerous, small, abundantly pubescent leaflets, long stipules, and pendent, incurved fruits. Character correlation suggests a single, reasonably coherent, though variable taxon.

It is probable that some of the variation of *Eysenhardtia polystachya* is due to present and/or past hybridization. This view is supported in that variation is geographically oriented with respect to the ranges of related species; only where *E. polystachya* overlaps with a given species does it assume some of the characters of that species. Examples follow. Specimens of *Eysenhardtia polystachya* from Durango have smaller leaves and more pubescent leaflets than those from other areas. Here the range overlaps with *E. spinosa* and *E. schizocalyx*, both of which have small, conspicuously pubescent leaflets. Specimens from the southern part of the range, Guerrero and Puebla, have large leaves and leaflets that are usually glabrescent. This is precisely where *E. polystachya* and *E. platycarpa* overlap, and the leaf characters mentioned are those of the latter species. Furthermore, mesophyll crystals are always found in *E. platycarpa*. In *E. polystachya* such crystals are borne by specimens only from (or near) areas of sympatry. A few ponderable specimens have the ascending fruits of *E. texana* and gland distribution of *E. polystachya* on some leaflets, but that of *E. texana* is on others. These specimens come from areas where both species grow.

Field observations support a hypothesis that *E. texana* and *E. polystachya* hybridize for both are visited by the same soldier beetles (Cantharidae; *Chauliognathus* sp.) and honey bees (*Apidae*) which could effect cross-pollination. Greenhouse evidence also suggests that the species under discussion might hybridize where contact is possible. *Eysenhardtia polystachya* seems to be an outcrossing species. Repeated efforts to self plants of *E. polystachya* from two populations failed to produce any fruit set. On the other hand, when pollinated by *E. texana* or *E. spinosa*, they showed good fruit set and produced some seed. In a reciprocal cross, the  $F_1$  progeny from *E. polystachya* (male)  $\times$  *E. spinosa* (female) had large leaves and numerous leaflets (23-35), more closely resembling the male parent (*E. polystachya*). Indeed, vegetative observations alone would suggest that the two parents could have been *E. polystachya*  $\times$  *E. schizocalyx* instead of the real parents *E. polystachya*  $\times$  *spinosa*.  $F_1$  flowers or fruits had not been produced when research was terminated.

The identification of the classic *Lignum nephriticum* with *Eysenhardtia polystachya* has previously been noted. Some of Safford's cited material (1915a, 1915b), however, is *E. texana*.

Though we have seen neither the *Eysenhardtia polystachya* nor the *E. amorphoidees* H.B.K. types, both are reasonably identifiable from original descriptions and figures, and the identity of *E. amorphoides* is verified from microform as cited.

*EYSENHARDTIA PUNCTATA* Pennell

*Eysenhardtia punctata* Pennell, N. Amer. Fl. 24: 39. 1919.

Type: Mexico, Jalisco: between Bolaños and Guadalajara, 19 Sept. 1897. *Rose* 3734. Holotype US!

A shrub or small tree, 3-5 m. Stems grayish to grayish-brown. Pubescence of incurved hairs. Leaves 3-10 cm, petiolules .5-.9 mm; leaflets 30-45, oblong-ovate, 5-13 mm, firm, glabrate to puberulent on both surfaces, dull-green above, paler beneath and punctate with large (sunken) internal cavities. Stipules 2-4.5 mm, stipels subulate, .4-1 mm, persistent. Racemes 4-9 mm; bracts deciduous. Calyx tube 2.5-4 mm, glandular-dotted, minutely puberulent, split deeply on the upper side, nearly to the base at fruit maturation; teeth .2-.5 mm, acute to rounded. Pedicels 1 mm. Petals 6-8 mm, membranous. Style 2.5-4 mm, with a thick, subdistal gland. Legumes ascending-spreading at maturity, shortly oblong or tapering in both directions, commonly slightly curved, 11-16 × 3-5 mm, thin, greenish-brown to dark brown. Seeds 4-5 mm, broadly oblanceolate, smooth, olive-brown to dark brown, filling one-third to one-half of the fruit.

Mexico: Jalisco, Queretaro, Aguascalientes, Puebla. Steep, open, brush-covered hills or in thorn-cactus desert scrub. Elevation: 1,600-2,000 (-2,500) m. Flowering: May-August. Fruiting: August-September.

*Eysenhardtia punctata* is a morphologically diverse species, presumably related to *E. adenostylis* and *E. platycarpa* which have similar, large, ascending-spreading fruits. *E. punctata* ideally differs from these other species in its smaller leaves whose leaflets are not lightened beneath by mamillate epidermal cells, and in its more diffusely open fruiting inflorescence. The leaflets have larger, less evenly distributed, glands than those of sympatric species. These glands are often deeply sunken in leaf mesophyll and only faintly visible externally.

By description, *Eysenhardtia punctata* differs, or may differ, from similar or sympatric species by a syndrome of several characters. Nevertheless, a considerable proportion of the specimens seen are atypical in one way or another. We suggest that there may be considerable gene exchange between *E. punctata* and *E. polystachya* throughout its range and with *E. platycarpa* in the western portion.

The holotype of *Eysenhardtia punctata* is possibly a hybrid between *E. punctata* and *E. platycarpa*, but we arbitrarily assign it to *E. punctata*.

*EYSENHARDTIA SCHIZOCALYX* Pennell

*Eysenhardtia schizocalyx* Pennell, N. Amer. Fl. 24: 39. 1919.

Type: Mexico, Durango: Mapimi, Durango and vicinity; 21-23 Oct. 1898. *Palmer* 528. Holotype NY! Isotypes F! MO! UC!

Virgately branched shrub or small tree. Stems gray to black. Pubescence of incurved or appressed hairs. Leaves 2-4 cm; leaflets 21-29, oblong-oblanceolate, narrowed at the base, round-apiculate at the apex, 4.5-6.1 × 2-3 mm, pale-green and appressed pubescent both above and below, punctate below. Stipules 1-2 mm; stipels .3-.6 mm. Racemes 5-10 cm; bracts canescent,

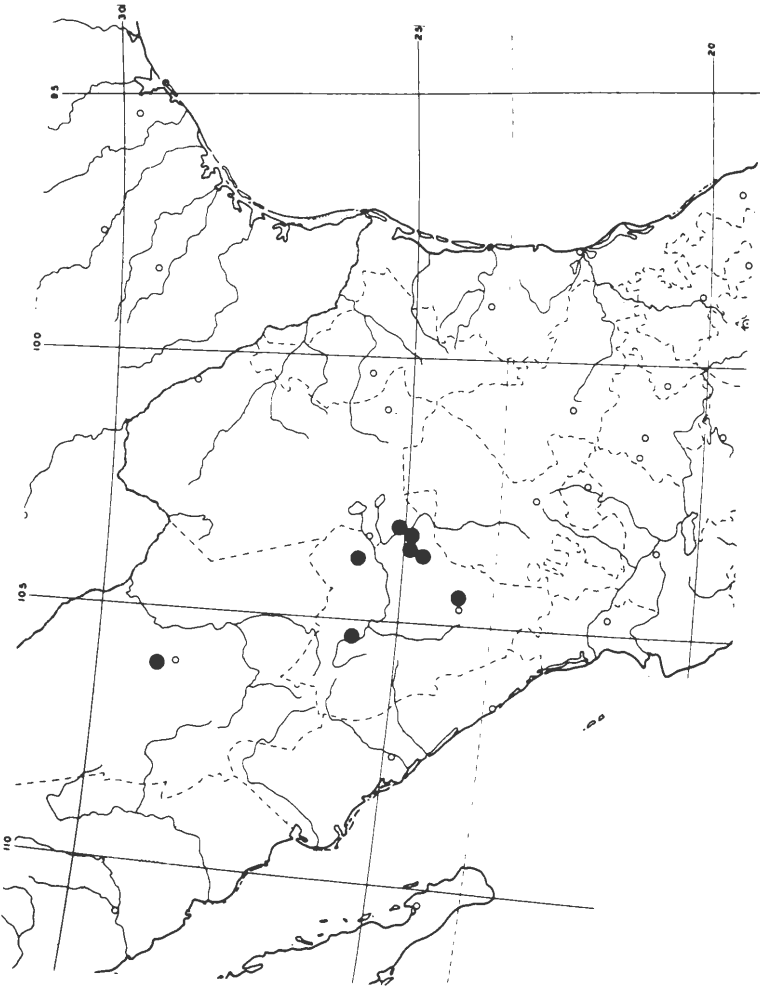


Figure 7. *Eysenhardtia schizocalyx*.

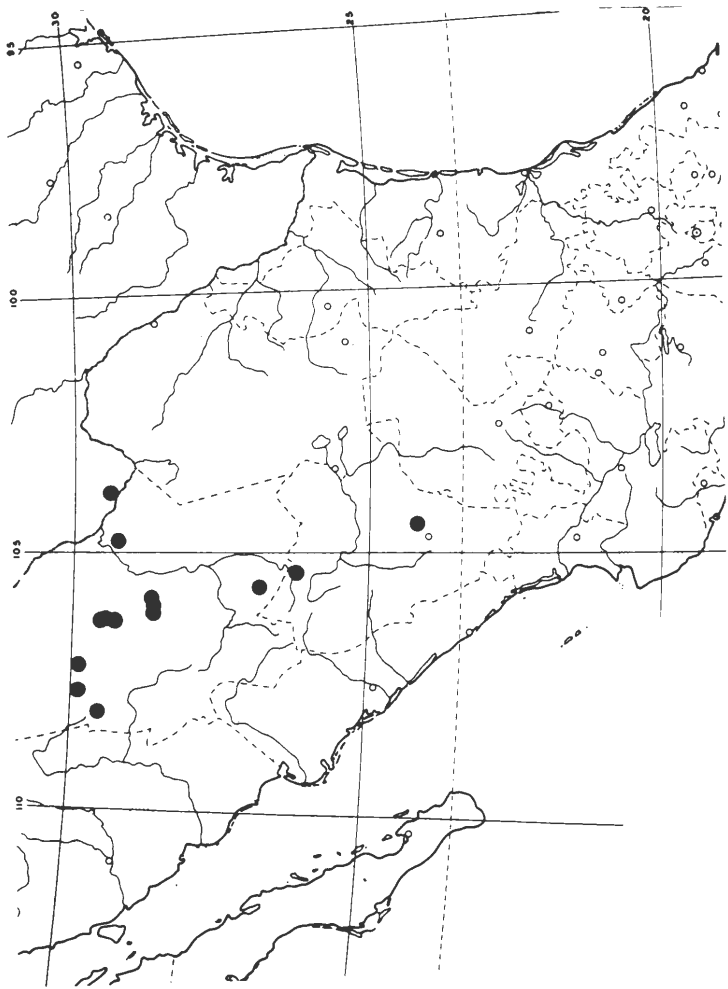


Figure 8. *Eysenhardtia spinosa*.

persistent. Pedicels ca. .5 mm. Calyx tube 1.5-3 mm, glandular-dotted, canescent, dorsally split to the base in mature fruit; calyx teeth .5-1 mm. Petals 5-7.2 mm, membranous. Style 2 mm, subterminally pubescent with long hairs, eglandular. Legumes slightly upcurved and ascending, elliptic, proximally rounded or apically pointed, 6-7.5  $\times$  2.5-3 mm, eglandular or inconspicuously glandular distally; sutures comparatively salient. Seeds 4 mm, thickened, oblanceolate, smooth, pale-brown, filling the entire fruit.

Mexico: Durango, Coahuila, and Chihuahua. Washes, pebbly stream beds and open stony hills. Elevation 650-1,600 (-2,100) m. Flowering: June-September. Fruiting: June-October.

This species can be readily recognized either in the flowering or fruiting condition. The virgate stems, the small, relatively few leaflets per leaf, the incurved calyx lobes, and the short fruits are distinctive.

The senior author has synthesized hybrids between *Eysenhardtia spinosa* and *E. polystachya*, which vegetatively resemble *E. schizocalyx*, and it is speculatively possible that the ancestry of *E. schizocalyx* might owe to these species. *E. spinosa* and *E. schizocalyx* are the only species which have calyces slit to the base and expanded in fruit and apically acute fruits with strongly developed sutures. *E. orthocarpa*, *E. polystachya*, and *E. texana* all might be eligible for the other putative parent but only *E. polystachya* is geographically available.

#### *EYSENHARDTIA SPINOSA* Engelm

*Eysenhardtia spinosa* Engelm. in Gray, Bost. Jour. Nat. Hist. 6 (2): 174. 1850! Type: Mexico: near Lake Encinillas, North of Chihuahua, 21 Aug. 1846. *Wislizenus* 133. Holotype GH! Isotype MO!

An intricately branched shrub to 1 m. Stems black. Pubescence of incurved or appressed hairs. Leaves 1-3 cm; leaflets 13-17, oblong-obovate, 3-5 mm, yellow-green, slightly thickened, glabrate to puberulent, glaucous beneath and punctate with small dark glands. Stipules 1-2 mm; stipels subulate, .2-7 mm, persistent,  $\pm$  the petiolules. Racemes 1-3 cm; bracts loosely canescent, persistent. Pedicels to .5 mm. Calyx-tube 2-3 mm, glandular-dotted, canescent, purple-tinted, ridged, and split to the base on the dorsal side at maturity; teeth acuminate, .5-9 mm. Petals 5-7.5 mm, firm, ochroleucous or almost white, eventually turning purple. Style 2-3 mm, densely pubescent, eglandular. Legumes ascending, elliptic, turgid, 5-6  $\times$  2-3 mm, ridge-veined, light brown, glandless or punctate distally with minute glands; sutures comparatively salient. Seeds 3-4 mm, obovoid, thick, laterally ridged, light brown, filling the entire fruit.

Mexico: Chihuahua, Durango. U.S.: Texas (Presidio Co.). Sloping rock outcrops or calcareous gravel flats in the Chihuahuan Desert or in the transition areas between the desert and the grama grasslands. Elevation 1,300-1,600 (-2,000) m. Flowering: April-September. Fruiting: May-September.

The closest relatives of *Eysenhardtia spinosa* are *E. schizocalyx*, *E. peninsularis*, and *E. parvifolia*. Although the cluster analyses paired *E. spinosa* with *E. parvifolia*, possibly due to similar leaf characters, we suspect that *E. spinosa* is more closely related to *E. schizocalyx* and conceivably one of its

parents (see *E. schizocalyx*). On the other hand, *E. spinosa* and *E. parvifolia* differ strikingly in fruit, those of the former being turgidly subspheroid when immature and keeled laterally by a protruding vein at maturity. The fruit glands of *E. parvifolia* are the largest in the genus, while those of *E. spinosa* are small and few (as in *E. schizocalyx*).

Englemann's description of *Eysenhardtia spinosa* specifies four ovules. We found two ovules, a number consistent with all that of other species of *Eysenhardtia*.

#### EYSENHARDTIA SUBCORIACEA Pennell

*Eysenhardtia subcoriacea* Pennell, N. Amer. Fl. 24: 36. 1919!

Mexico, Hildago: Ixmiquilpan, Aug. 1905. *Purpus* 1366.

Holotype NY!

A shrub or small tree, 3-8 m. Stems grayish-brown. Pubescence of incurved or appressed hairs. Leaves 3-11 cm; leaflets 19-37, oblong, firm, 6-15 mm, pubescent both sides, dull-green above, pale and punctate beneath with minute brown glands. Stipules 1.7-4.2 mm, stipels subulate, .4-1.4 mm, persistent. Racemes 3-9 cm; bracts deciduous. Pedicels .5-1 mm. Calyx-tube 2.5-3.5 mm, glandular-dotted, canescent, shallowly split on dorsal side; teeth .3-.7 mm, acute to obtuse. Petals 6-7 mm, firm. Style 3-4 mm, subterminal gland small or large. Legumes reflexed-spreading at maturity, oblong-lanceolate, 11-16 × 2.8-4 mm, thin, greenish-brown, punctate distally with small glands. Seed filling two-fifths of pod.

Mexico: central Oaxaca northwest to Puebla and Hidalgo. Habitat unknown. Flowering: July-October. Fruiting: August-October.

*Eysenhardtia subcoriacea*, though reasonably distinctive, must be regarded with reservation. These plants are variously intermediate between *E. polystachya* and *E. punctata*, and the specimens come from the area of sympatry of these species.

Possibly *Eysenhardtia subcoriacea* represents no more than  $F_1$ , or perhaps derivative, hybrids between *E. polystachya* and *E. punctata*. Specific status is maintained pending more knowledge of its relationships.

#### EYSENHARDTIA TEXANA Scheele

*Eysenhardtia texana* Scheele, Linnaea 21: 462. 1848. Type:

United States, Texas: An hohen Ufferänd and trocken Plätzen in der Nahe des Wasser bei Neubraunfels, July, Aug., Sept. 1846. *Lindheimer* 268 (*Gray* 374). Holotype MO! Probable isotypes: NY! SMU!

*Eysenhardtia angustifolia* Pennell, N. Amer. Fl. 24: 38. 1919.

Type: United States, Texas (Terrell Co.): Sanderson, 29 Sept. 1911. *Wootton s. n.* Holotype US!

Basally branching, small tree or shrub, 1-3 (-5) m. Stems grayish to grayish-brown. Pubescence of incurved-appressed hairs. Leaves 3-10 cm, leaflets 15-47, oblong to narrowly oblong, 4-13 mm, puberulent, firm, dull-green

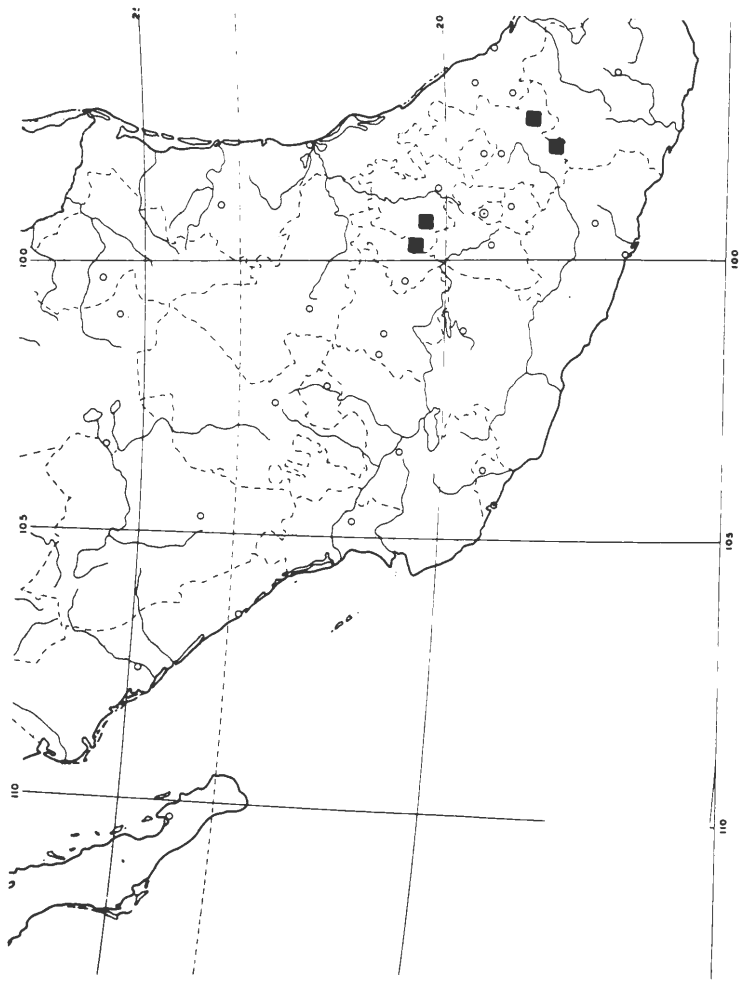


Figure 9. *Eysenhardtia subcoriacea*.

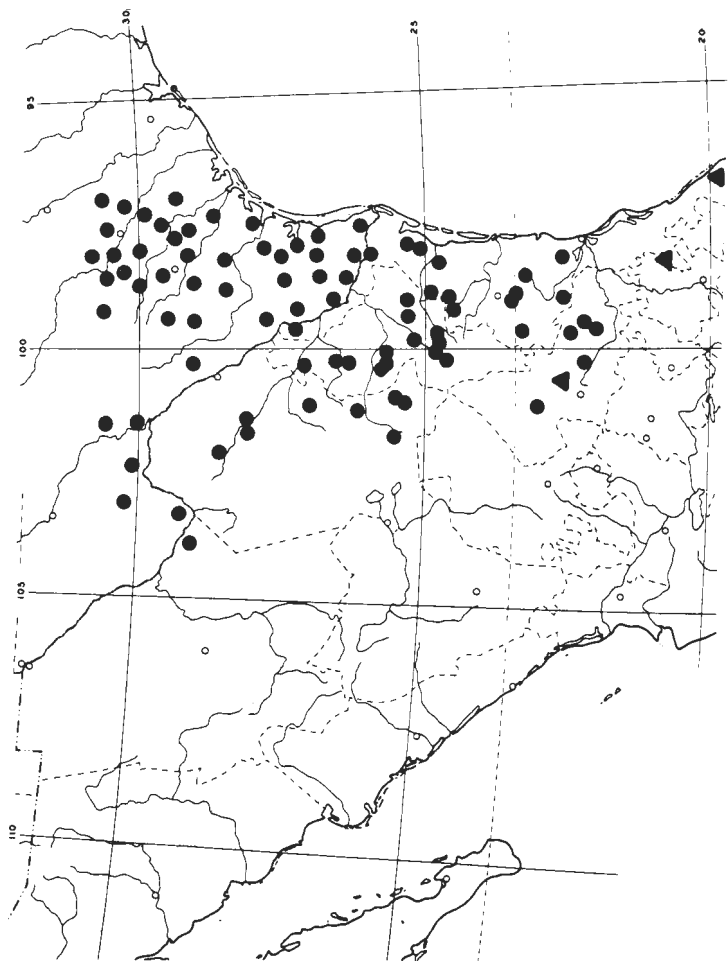


Figure 10. *Eysenhardtia texana* O; *E. texana* X *polystachya* (putative) Δ.



above, beneath slightly paler and punctate with large glands along and near the midrib and intercalary smaller ones. Stipules 1.5-5.5 (-6.5) mm; stipels subulate, .2-.8 mm long,  $<$  or  $=$  the petiolules (rarely longer in a few suspected hybrids from Tamaulipas and southward). Racemes 3-11 cm; bracts persistent. Pedicels .5-2 mm. Calyx-tube 2-4 mm, glandular-dotted, canescent, slightly ridged, shallowly split on the posterior side or not; teeth .3-.7 mm, obtuse to acute. Petals 5-8 mm, membranous. Style 2.5-3 mm; subterminal gland thick, conspicuous (absent on a few putative hybrids from Tamaulipas and southward). Legumes oblong-upcurved, ascending,  $6-13 \times 1.7-3.7$  mm, greenish-brown, punctate distally with evident glands. Seeds 3.2-3.7 mm, curved-lanceolate, thickened, smooth, light brown, filling two-thirds of the fruit.

United States: Central and west Texas from Bell to Brewster Cos. Mexico: Eastern states south to San Luis Potosi and Veracruz. Gullies, arroyos, in desert chaparral and cedar-shinoak; sand, clay, caliche. Elevation 1,000-1,600 (-2,500) m. Flowering: April-November. Fruiting: May-December.

*Eysenhardtia texana* is sympatric with the widely distributed *E. polystachya* in southern Tamaulipas, San Luis Potosi and northern Veracruz. Like most other species of *Eysenhardtia*, it apparently hybridizes with *E. polystachya*. The primary evidence, as stated elsewhere, is that intermediate forms are found only where the two species are sympatric or nearly so.

Pennell's (1919) differentiation of *Eysenhardtia texana* and *E. angustifolia* is insubstantial. Leaf length, his primary character, forms a continuum; the same is true of most of the other differential characters mentioned, which, in any case, do not correlate.

Major herbaria contain Lindheimer gatherings of *Eysenhardtia texana* from New Braunfels bearing several accession numbers and dates between 1846 and 1850. All of them are the species concerned. Technical designation of the holotype and isotypes, however, requires care. Among several options, a MO specimen is the most apodictic representation of the type. It bears Lindheimer's original label (No. 268), and the data is directly copied by Scheele in the protologue quoted above. This sheet also is labeled Gray No. 374, as are Lindheimer specimens of *E. texana* in other herbaria. But not all of this material is isotypic because of Gray's practice of distributing more than one collection of a species under one exsiccatae number. Only those bearing the Lindheimer number, or if not, the year 1846 (the introduction to Scheele's paper specifies that his Lindheimer material was of this year), are probable isotypes.

We have called the above named MO Lindheimer specimen the holotype, but the considerations of choice to some degree spell lectotypification.

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## THE KNOWN PRATYLENCHIDAE (NEMATODA) OF IOWA<sup>1</sup>

D. D. Williams<sup>2</sup>

**ABSTRACT.** During 1979 and 1980, seven species of the Pratylenchidae were collected from 118 plants from 38 counties in Iowa. The nematodes and plant associates were: *Hirschmanniella gracilis* (cattail); *Pratylenchoides erzurumensis* (giant ragweed); *Pratylenchus alleni* (corn); *P. flakkensis* (corn, plantain, giant ragweed, soybean, sunflowers); *P. bexincisus* (corn, foxtail, soybean, plantain); *P. neglectus* (corn); and *P. scribneri* (corn, soybean, foxtail, giant ragweed). *Pratylenchus bexincisus* was collected most frequently and probably occurs statewide. The largest nematode populations were those of *P. scribneri* and *P. bexincisus* in the southeastern counties.

Additional index words: *Hirschmanniella gracilis*; *Pratylenchoides erzurumensis*; *P. alleni*; *P. flakkensis*; *P. bexincisus*; *P. neglectus*; *P. scribneri*.

## INTRODUCTION

The nematode family, Pratylenchidae, comprises nearly one hundred species distributed among seven genera (*Hirschmanniella* (Luc and Goodey); *Hoplotylus* s'Jacob; *Pratylenchoides* Winslow; *Pratylenchus* Filipjev; *Radopholoides* de Guiran; *Radopholus* Thorne; and *Zygotylenchus* Siddiqui). Some of the Pratylenchidae (species of *Pratylenchus*, *Radopholus*, and *Hirschmanniella*) are important endoparasites causing death, decline, or lack of vigor in plants. Seven species of the Pratylenchidae have been reported in Iowa: *Pratylenchus alleni*, *P. convallariae*, *P. coffeae*, *P. bexincisus*, *P. neglectus* (= *P. minyus*), *P. penetrans*, and *P. vulnus* (Burns, 1971; Norton and Burns, 1971; Norton and Hinz, 1976; Norton et al., 1964, 1978; Schmitt, 1973; Thomas, 1978; Zirakparvar, 1980). Because some of these reports are documented neither by extant specimens nor morphometric analysis, this study was initiated to re-evaluate which species occur in Iowa with emphasis on those affecting corn (*Zea mays*). The listing following includes only those species validated by this work.

## MATERIALS AND METHODS

One hundred and eighteen root samples from seven species of plants (101 samples from field corn) were collected in 38 Iowa counties representing

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all parts of the state in September, 1979, and July and August, 1980. Nematodes were removed from washed 1- to 2-cm long root segments of plants by the 96-hr shaker method (Bird, 1971), preserved in a 1.5% methanol-water solution after heating for 20 minutes at 39° C, and either observed microscopically in preservative or placed in glycerol (Seinhorst, 1959) for permanence. The descriptions are based on measurements of Iowa specimens obtained during this study. Mean measurements are given, with minimum and maximum in parentheses. Abbreviations are N (sample size), L (length), a (length of nematode divided by greatest width), b (length of nematode divided by esophagus length), c (length of nematode divided by tail length), and V (vulva position as a percentage of body length from anterior).

## RESULTS AND DISCUSSION

### *Hirschmanniella*

Generic diagnosis: Adults 900 to 4,200  $\mu\text{m}$  in length; lip region well developed, continuous with body contour; esophageal glands overlap intestine ventrally; four incisures in lateral field; ovaries paired; tail tapering to a point or mucro.

#### *Hirschmanniella gracilis* (de Man) Luc and Goodey

N = 27 females: L = 1,482  $\mu\text{m}$  (1,396-1,759); a = 54 (53-58); b = 12.6 (11-14); c = 15 (14-16.5); V = 52 (51-54); stylet = 20  $\mu\text{m}$  (19-21); three to four indistinct lip annules.

N = 5 males: L = 1,510  $\mu\text{m}$  (1,480-1,670); a = 49 (42-54); b = 12.8 (12-13); c = 18 (17-20); stylet = 19  $\mu\text{m}$  (18-20); spicules = 33  $\mu\text{m}$  (29-37); three to four indistinct lip annules.

Associated plant: *Typha* sp., Hamilton County, Little Wall Lake.

### *Pratylenchoides*

Generic diagnosis: Length 500 to 1,200  $\mu\text{m}$ ; labial framework well developed; lips with two to five annules, continuous with body contour; deirids present; sexual dimorphism present in anterior part of body; esophageal glands overlap intestine dorsally, laterally, and ventrally; ovaries paired; lateral incisures four or six; phasmids present.

#### *Pratylenchoides erzurumensis* Yuksel

N = 12 females: L = 730  $\mu\text{m}$  (649-864); a = 25 (25-26); b = 4.1 (4.0-4.5); c = 15 (13-16); V = 55 (53-59); stylet = 21  $\mu\text{m}$  (20-22); tail annules = 26 (23-30); lip region flattened anteriorly; three or four striae; four or five lip annules; esophageal glands conspicuous; lateral field with six median incisures and four incisures in anterior and posterior body regions; tail indented with none to four striations at terminus. Males unknown.

Specimens of *P. erzurumensis* from Turkey possess three or four lip annules, whereas those from Iowa possess four or five lip annules.

Associated plant: *Ambrosia trifida* L., Story County, Washington Township.

*Pratylenchus*

Generic diagnosis: Length less than 1,000  $\mu\text{m}$ ; lip region well developed, with two to four annules; incisures four to six, rarely seven or eight; esophagus overlaps intestine ventral-laterally; ovary single; tail bluntly rounded, males present in some species.

*Pratylenchus allenii* Ferris

N = 106 females: L = 402  $\mu\text{m}$  (347-614); a = 24 (18-29); b = 4.5 (4.0-6.3); c = 21 (15-26); V = 80 (77-83); distance, anus to tail terminus = 22  $\mu\text{m}$  (19-27); tail annules = 17 (15-21); stylet = 14  $\mu\text{m}$  (12.6-16.3); spermatheca present, spherical or pyriform in shape; two lip annules; tail crenate, occasionally smooth, lateral field with four incisures.

N = 84 males: L = 382  $\mu\text{m}$  (310-414); a = 27 (21-33); b = 5.4 (4.8-6.3); c = 21 (17-23); stylet = 13  $\mu\text{m}$  (12-25); spicules = 15  $\mu\text{m}$  (14-17); two lip annules.

Associated plants: Corn (*Zea mays*). *P. allenii* was present in 12 of the 38 counties in which collections were made (Adair, Allamakee, Black Hawk, Boone, Bremer, Cass, Cherokee, Clinton, Jasper, Madison, Story, and Webster counties). Populations ranged from 7,441 and 2,141 nematodes/g of dried root in Jasper and Webster counties, respectively, to fewer than 60 nematodes/g of dried root in all other locations. No *P. allenii* were obtained from other plants. In Illinois, however, populations ranged from 515 to 1,914 nematodes/g of dried soybean (*Glycine max*) root (Ferris and Bernard, 1958).

*Pratylenchus flakkensis* Seinhorst

N = 178 females: L = 508  $\mu\text{m}$  (309-620); a = 25 (20-27); b = 5.3 (5.7-7.3); c = 17.3 (13-23); V = 78 (75-89); distance, anus to tail terminus = 28  $\mu\text{m}$  (26.6-32.9); tail annules = 21 (16-23); stylet = 17  $\mu\text{m}$  (15-18), slender with knobs occasionally cupped; spermatheca spherical, occasionally ellipsoidal or pyriform; two lip annules; tail crenate, occasionally smooth; lateral field with four incisures.

N = 58 males: L = 446  $\mu\text{m}$  (327-486); a = 25 (19-27); b = 5.3 (5.0-6.4); c = 18 (16-21); stylet = 16  $\mu\text{m}$  (14-17), spicules = 14  $\mu\text{m}$  (14-16); two lip annules.

Associated plants: Sunflower (*Helianthus* sp), plantain (*Plantago major*), and corn. Nematodes/g of dried root, ca. 1100, 100, 100, respectively. Hamilton, Linn, Story, and Winnebago counties. Males accounted for 2 to 60% of a population. *Pratylenchus flakkensis* has been previously reported from Iowa (Thomas, 1980).

*Pratylenchus bexincisus* Taylor and Jenkins

N = 276 females: L = 478  $\mu\text{m}$  (372-726); a = 23 (17-28); b = 5.0 (4.6-8.5); c = 20 (15-24); V = 79 (75-83); distance, anus to tail terminus = 28  $\mu\text{m}$  (21-33); tail annules = 21 (17-25); stylet = 16  $\mu\text{m}$  (13.8-27.3); spermatheca not observed; tail terminus generally smooth; lateral field consists of six, occasionally seven, or rarely eight, continuous incisures except at midbody where incisures often are broken irregular lines; two lip annules; males were absent from collections.

Associated plants: Corn. Nematodes/g of dried root ca. 10-10,000. Found in 36 of 38 counties.

In Osceola and Lee counties (Zirakparvar, 1979; Norton and Hinz), *P. hexincisus* accounted for 95% of the *Pratylenchus* recovered from roots. The host range and pathogenicity of *P. hexincisus* have been studied experimentally (Zirakparvar, 1980).

*Pratylenchus neglectus* (Rensch) Filipjev and Schuurmans Stekhoven

N = 27 females: L = 478  $\mu$ m (306-538); a = 22 (18-25); b = 5.4 (4.2-5.8); c = 19 (17-21); V = 78 (77-82); distance, anus to tail terminus = 24  $\mu$ m (23.4-25.4); tail annules = 19 (16-28); stylet = 16  $\mu$ m (15-17); spermatheca not observed; two lip annules; tail terminus without striations; males were absent.

Associated plants: Corn: 3,970 and 509 nematodes/g of dried root. Benton and Lee counties, respectively.

*Pratylenchus scribneri* Steiner

N = 74 females: L = 550  $\mu$ m (360-628); a = 23 (17-25); b = 5.6 (5.1-6.6); c = 17 (15-18); V = 78 (75-83); distance, anus to tail terminus = 24  $\mu$ m (20-31); tail annules = 23 (19-24); stylet = 15  $\mu$ m (14-17); spermatheca not observed; two lip annules; tail smooth, rarely crenate; males were not present.

Associated plants: Corn: up to 44,000 nematodes/g of dried root. Foxtail (*Setaria* sp): from 4 to (usually) several hundred nematodes/g of dried root. Des Moines, Lee, and Louisa counties (southeastern Iowa), Story and Marshall counties (central Iowa), and Union County.

*Pratylenchus vulnus* Allen and Jensen

Lilac (*Syringa vulgaris*). Shenandoah in Page County. This record consists of two specimens, a male and a female, on a single slide, collected by D. Schmitt (Iowa State University Nematode Collection). No *P. vulnus* was obtained during this study.

## KEY TO SPECIES OF THE PRATYLENCHIDAE KNOWN IN IOWA

1. Ovaries paired . . . . . 2  
Ovary single. . . . . 3
2. Deirids absent, tail tip mucronate . . . . . *Hirschmanniella gracilis*  
Deirids present, tail tip not mucronate . . . . . *Pratylenchoides erzurumensis*
3. Lip annules 3 or 4 . . . . . *Pratylenchus vulnus*  
Lip annules 2. . . . . 4
4. Lateral field with five or more incisures . . . . . 5  
Lateral field with four incisures (occasionally  
a faint fifth incisure present). . . . . 6
5. Incisures six, occasionally seven, rarely eight. . . . . *Pratylenchus hexincisus*  
Incisures five, the fifth being a broken diagonal . . . . . *Pratylenchus neglectus*
6. Males absent, spermatheca not observed  
or empty . . . . . *Pratylenchus scribneri*  
Males present. . . . . 7

7. Stylet 14 to 18  $\mu\text{m}$ , usually 16  $\mu\text{m}$  or more,  
 tail annules 16-24 (usually 18 or more) . . . . . *Pratylenchus flakkensis*  
 Stylet 13 to 16  $\mu\text{m}$ , usually less than 15;  
 tail annules 15-21 (usually 17 or less) . . . . . *Pratylenchus alleni*

Three other *Pratylenchus* species have previously been reported in Iowa (Norton et al., 1964). *Pratylenchus penetrans* Cobb was said to be widely distributed in Iowa. *P. convallariae* Seinhorst "was found twice. . ." but specimens are no longer extant. *P. coffeae* Zimmerman was "found once in *Fragaria* in southwestern Iowa and once in *Narcissus*," but, again, specimens are not extant. In the present study, because few plants other than corn were sampled, it is probable that other species of the Pratylenchidae exist in Iowa.

After study of several thousand specimens of *Pratylenchus*, I conclude that several characters, listed as follows, are more reliable than others in differentiating the species in Iowa: number of lip annules, length of stylet, number and arrangement of lateral incisures, presence of males, and number of tail annules.

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## A SEED CORN MAGGOT TRAP FOR USE IN ROW CROPS<sup>1</sup>

G. M. Ghidui<sup>2</sup> and E. C. Berry<sup>3</sup>

**ABSTRACT.** A trap was constructed to capture seed corn maggot adults (*Hylemya platura* Meigen) by using commercial 12.5-cm galvanized rain gutter. The trap was more effective in capturing emerging seed corn maggot adults (SCM) in field corn than a previously described SCM pail trap. Galvanized rain gutter is durable and rust resistant, making this trap ideal for the capture of SCM and other positively phototactic soil insects throughout the growing season.

The seed corn maggot (SCM), *Hylemya platura* Meigen, is one of the first corn insect pests to appear in Iowa during early spring. SCM adults are attracted to freshly cultivated soil and stimulated to oviposit presumably because of the exposure to warm, moist soil (Miles, 1950; Reid, 1940). Eggs are deposited in the soil, and the developing larvae feed on germinating corn seeds.

Various traps and baits have been employed to determine numbers of emerging SCM adults (Miles, 1951; Eckenrode and Chapman, 1971). Most of these traps were designed to determine population peaks and thus were either large and cumbersome or time-consuming to use. Miller and McClanahan (1960) described a simple, inexpensive SCM trap employed to determine the number of generations and the emergence period for each generation. However, a trapping technique has yet been needed to effectively determine the numbers of emerging SCM adults in field corn planted under various amounts of surface residue. We modified the trap described by Funderburk and Pedigo (1980) for this purpose.

## MATERIALS AND METHODS

Miller and McClanahan's trap consisted of an inverted 7.6-ℓ sap pail with a glass vial fitted into a hole punched near the upper end of the upturned pail. Miller's trap was modified to a 19.0-ℓ pail, which increased surface area covered, and a 0.47-ℓ screw-top Mason jar was attached to the upper end. A second SCM emergence trap was constructed from commercial 15.2-cm galvanized rain gutter cut into 1-m sections to increase the row length covered by a trap. Left and right end caps were attached by using 2.54-cm corner braces

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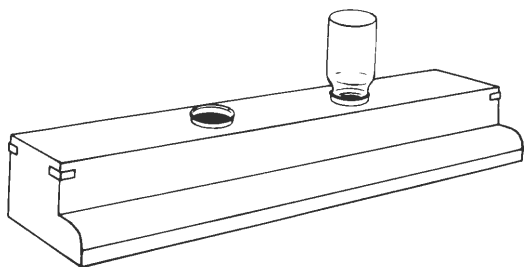


Figure 1. The "rain-gutter" seed corn maggot trap.

and 1.27-cm x 8/32 bolts. Two 3.81-cm holes were cut in the gutter bottoms, each ca. 30 cm from the end, and a 0.47-l screw-type mason jar was attached externally by riveting a ring over each hole (Fig. 1). Elastic caulking compound was used on the inner surface to seal the end caps and jar rings, thereby preventing light seepage into the traps.

Each trap was forced into the soil to a depth of ca. 7.6 cm, and an additional 7.6 cm of loose soil was placed along the sides and ends. The positively phototactic adults emerged into the Mason jars, which were then removed every second day, capped for later identification, and replaced with empty jars.

A 5-ha cornfield with varying amounts of surface residue was planted May 17 on 76-cm centers. On May 26, 60 of each trap (the "rain gutter" and the "pail") were placed in the field (five traps/0.5 ha); one of each was centered over the row next to the other. The total number of flies per trap was recorded every second day for five weeks.

These studies were part of an ongoing experiment and were conducted to determine total flies captured over time in each trap type; no efforts were made to determine number of generations or population peaks. To determine if a difference existed in mean capture between traps, an observed *t*-value was calculated (Steele and Torrie, 1960) and compared with the tabulated *t*-value.

## RESULTS AND DISCUSSION

Over the five-week period, a total of 77 and 21 SCM adults were captured in the rain gutter and pail traps, respectively. The total capture from each 0.5 ha plot (five traps/ha) was used to compute the standard deviation, standard error of the mean difference, and the observed *t*-value. The mean capture of SCM adults with the rain-gutter traps was significantly greater than the inverted pail traps at the one percent probability level (observed *t* = 3.40; theoretical *t* = 3.06).

The 1-m rain-gutter trap covers ca. three times more surface area than the pail trap, which may explain the significantly larger number of SCM adults which it captured. The rain-gutter traps are quickly and easily constructed from commercially available sources in lengths up to the 6.1 m. The trap width of 15.2 cm enables SCM adults emerging from the seed zone to be trapped, yet allows many row-crop cultivators to pass over it without interference. Also, rain gutter is either aluminum or galvanized steel, thus making it weather-resistant; the pail traps began rusting soon after being placed in the field.

The rain-gutter trap may possibly be employed to trap other positively phototactic soil insects.

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PRESENT STATUS OF INTRODUCED PARASITOIDS OF THE  
EUROPEAN CORN BORER, *OSTRINIA NUBILALIS*  
(HÜBNER), IN IOWA<sup>1, 2</sup>

L. C. Lewis<sup>3</sup>

**ABSTRACT.** *Eriborus terebrans* (Gravenhorst), *Lydella thompsoni* Herting, and *Macrocentrus grandii* Goidanich were released in Iowa between 1944 and 1951. A small percentage of the diapausing population of the European corn borer has been parasitized by *E. terebrans* and *M. grandii* each year since 1954. Presently, these parasitoids occur in low numbers over a wide area of Iowa. Of these three parasitoids, *L. thompsoni* was the most prevalent throughout the state until 1962, when populations began to decline. *L. thompsoni* has not been found in Iowa since 1966. Possible reasons for the small populations of *E. terebrans* and *M. grandii* and the disappearance of *L. thompsoni* are discussed.

Additional index words: Parasitoids, European corn borer, *Lydella thompsoni*, *Eriborus terebrans*, *Macrocentrus grandii*.

## INTRODUCTION

The European corn borer, *Ostrinia nubilalis* (Hübner), was in Iowa in 1942 (Harris and Brindley, 1942). A substantial program of parasitoid introductions against *O. nubilalis* began in 1944 and continued through 1951 with the aim of reducing populations of this pest (Blickenstaff et al., 1953; Baker et al., 1949). Those species released in the largest number were: an ichneumonid wasp, *Eriborus terebrans* (Gravenhorst) (= *Horogenes punctorius* (Roman)), ca 17,000 released; a tachinid fly, *Lydella thompsoni* Herting (= *Grisecens* Robineau-Desvoidy auth.), ca. 55,000 released; and a braconid wasp, *Macrocentrus grandii* Goidanich (= *gifuensis* Ashmead), ca 730,000 released. Herein, I present and discuss the current status of these parasitoids in Iowa.

## METHODS AND MATERIALS

Annually, in the early fall (1951 to 1980), European corn borer larvae were collected from randomly selected corn fields in each Iowa county or crop reporting district. Counts of corn borer-infested plants were made from single 25-plant samples, taken 25 rows into each corn field. Two infested plants per

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<sup>1</sup> Lepidoptera: Pyralidae.

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field were dissected, and the collected larvae were returned to the laboratory and stored at 5° C and 75% RH. After about three months, the larvae were incubated at 27° C and 75% RH, one per screen-capped 1-dr shell vial containing a strip of wet blotter paper. At weekly intervals, the vials were checked for dead larvae, parasitoids, and corn borer pupae.

## RESULTS

*Eriborus terebrans* was released in 21 counties between 1944 and 1948, mostly in the southeastern quadrant of the state but also including Allamakee, Hancock, and Harrison counties (Fig. 1). Since 1951, *E. terebrans* has been recovered in 69 counties. From 1951 through 1959, the numbers of this parasitoid were negligible (Table 1). Those recovered were only from eastern Iowa until 1958, when a few were obtained from north-central and northwestern fields. Since 1959, *E. terebrans* has been found in most areas, but the majority, especially in the past three years, came from the western half of the state (Fig. 2).

*Macrocentrus grandii* was released in 83 counties between 1944 and 1951 and has been recovered in 80 counties since 1950 (Fig. 3). Following early findings, primarily in eastern Iowa, there has been a gradual increase in recoveries in the north-central area. By 1969, it was established in most of the eastern two-thirds of the state. There has also been an apparent increase in abundance. Less than 5% of the collected corn borers were parasitized by *M. grandii* through 1963. From 1964–1980, however, parasitization ranged from 0.29 to 56.22%. Although this species was not found for several years after its release, it has become the predominant parasitoid of the European corn borer in Iowa since the mid-1960s.

*Lydella thompsoni* was released in 52 counties between 1944 and 1951 and in Sioux and Clay counties in 1955 (Fig. 4). It was the most frequently recovered parasitoid from 1951 through 1959, being found predominantly in the eastern half of the state the first few years and then randomly throughout the state until 1962. Then, there was an abrupt decline in its prevalence. In 1963, it was found only in counties west of Story County and in 1964 only in Harrison, Shelby, Pottawattamie, Mills, and Fremont counties in extreme southwestern Iowa. *L. thompsoni* has not been collected in Iowa since 1966.

## DISCUSSION

Parasitoids of the European corn borer have been established in corn-growing regions of North America other than Iowa. *E. terebrans*, *L. thompsoni*, and *Sympiesis viridula* (Thomson) (= *Eulophus viridulus*) occur widely in southwestern Ontario, Canada (Wressell, 1973) and have been established in Nebraska (Hill et al., 1978). *L. thompsoni* was established in Delaware, disappeared and was reintroduced and established (Burbutis et al., 1981). Though these parasitoids, however, are generally of minor importance in suppressing corn borer populations in these areas, some exceptional rates of parasitization by *L. thompsoni* are on record: i.e., 75% in a corn field in DuPage County, Illinois (Brindley and Dicke, 1963) and 68% in Erie County, Ohio in 1953, with a state average of 33.5% (York and Carter, 1956). *M. grandii* parasitized

Table 1. Percentage parasitization of European corn borer larvae collected annually during the fall, 1951–1980.

Year	Number of European corn borer larvae collected	% larvae parasitized		
		<i>Eriborus terebrans</i>	<i>Macrocentrus grandii</i>	<i>Lydella thompsoni</i>
1951	1843	0.16	---	9.12
1952	1913	---	0.05	20.60
1953	1596	0.13	---	7.39
1954	3558	0.14	0.03	15.12
1955	1985	0.25	0.15	3.38
1956	4015	0.62	0.77	7.47
1957	5358	0.13	3.04	6.72
1958	3116	0.71	0.16	15.95
1959	3911	1.05	0.15	11.53
1960	8353	2.67	0.29	1.16
1961	14241	1.50	0.13	1.05
1962	5903	2.07	0.64	0.30
1963	7574	3.51	0.37	0.21
1964	292	6.51	5.82	2.05
1965	180	2.78	5.56	---
1966	5666	4.85	1.08	0.04
1967	136	3.68	16.18	---
1968	15702	4.81	7.20	---
1969	7468	8.57	32.73	---
1970	5983	2.67	8.26	---
1971	5277	0.11	37.03	---
1972	5053	0.04	56.22	---
1973	7422	0.12	11.01	---
1974	5383	0.84	4.03	---
1975	3839	8.93	0.29	---
1976	231	1.30	5.19	---
1977	582	2.06	6.01	---
1978	225	3.11	19.11	---
1979	198	2.53	21.72	---
1980	293	2.73	9.56	---



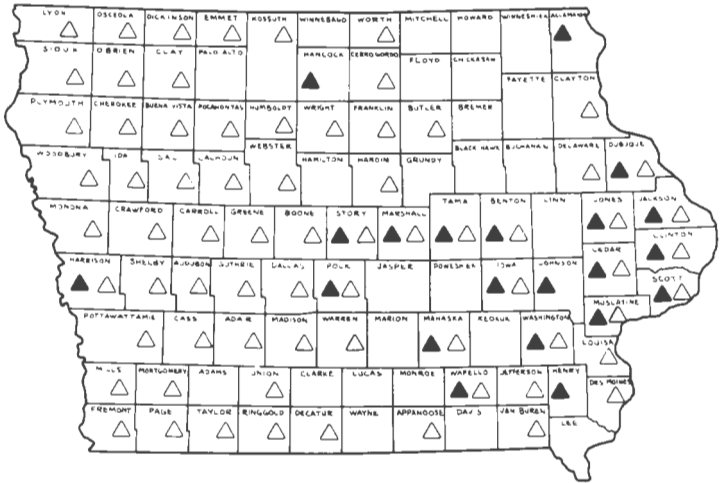


Figure 1. Counties in Iowa where *Eriborus terebrans* was released (closed triangles) and recovered (open triangles).

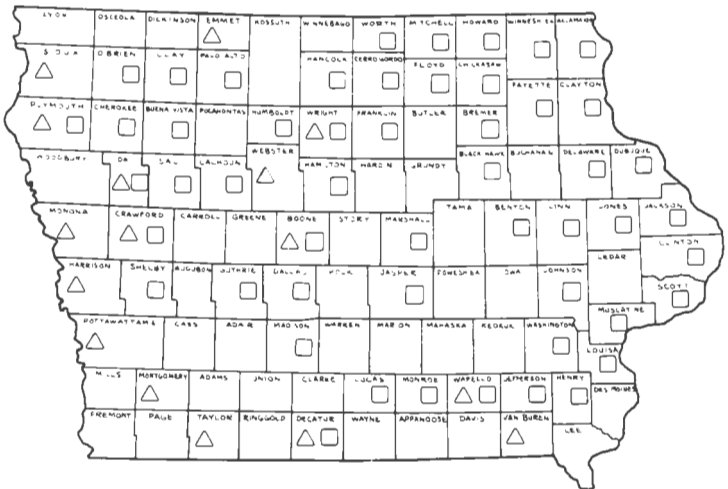


Figure 2. Counties in Iowa where *Eriborus terebrans* (triangles) and *Macrocentrus grandii* (rectangles) were recovered in 1978, 1979, and (or) 1980.

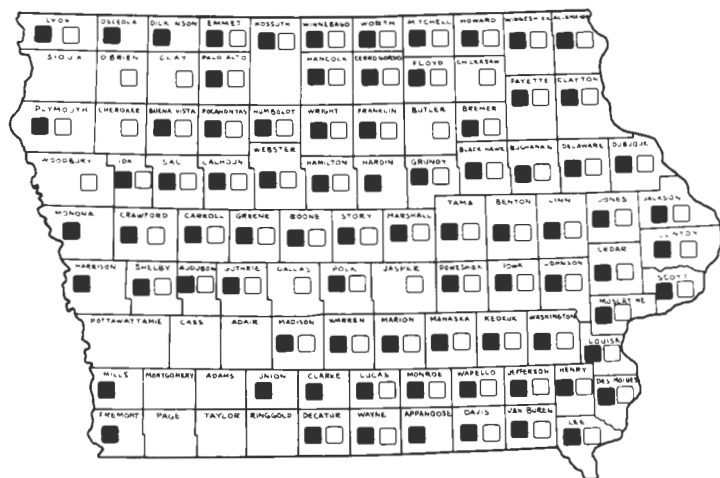


Figure 3. Counties in Iowa where *Macrocentrus grandii* was released (closed rectangles) and recovered (open rectangles).

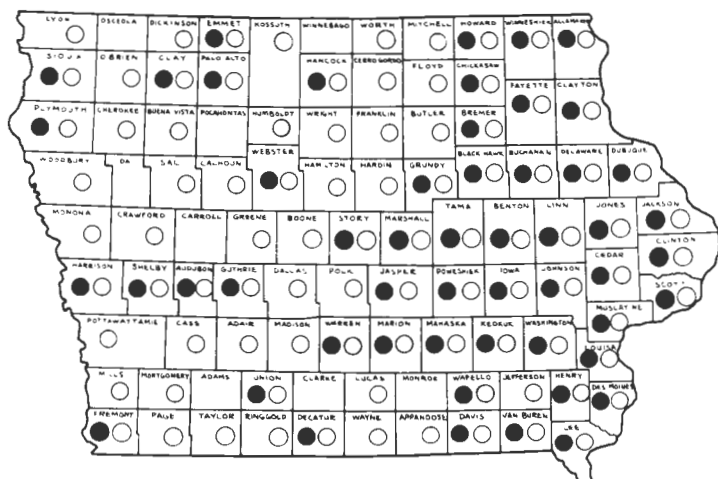


Figure 4. Counties in Iowa where *Lydella thompsoni* was released (closed circles) and recovered (open circles).

18 to 25% of the larvae collected in the period 1952–1954 in southern New England (York and Carter, 1956).

Regardless of their role in corn borer population suppression, *E. terebrans* and *M. grandii* are established in Iowa (Table 1; Figures 1, 2, and 3). The intriguing question is, why has *L. thompsoni*, a very promising parasitoid in Iowa and other locations, disappeared?

Several criteria must be fulfilled for successful establishment of exotic parasitoids: e.g., beyond suitable climatic conditions, the facts that the parasitoid must have good searching ability, that the life cycles of the parasitoid and host must be synchronized, and that the parasitoid should be able to distinguish diseased hosts and (or) previously parasitized hosts from healthy unparasitized hosts.

York et al. (1955) reported poor life-cycle synchronization between *L. thompsoni* and the corn borer. *L. thompsoni* adults emerging from overwintering corn borer larvae are ready to larviposit at least 10 to 14 days before any new corn borer larvae are suitable hosts (3rd- or 4th-instar). These authors reared *L. thompsoni* from larvae of the stalk borer, *Papaipema nebris* (Guenée), and speculated that it serves as an alternative host for *L. thompsoni*. Sparks et al. (1963) suggested that fluctuations in populations of *L. thompsoni* in Boone County, Iowa, were the result of fluctuations in populations of the stalk borer. The lotus borer, *Ostrinia penitalis* (Grote), also is an alternative host of *L. thompsoni* (Schaffner, 1953). If *L. thompsoni* is dependent on these two insects as supplemental hosts during late May and early June, then their infrequent occurrences would be detrimental to the survival of this parasitoid.

The pathogenic microorganisms of some phytophagous insects are known to infect their parasitoids and predators also. *Nosema pyrausta* (Paillot), a microsporidium, occurs in *M. grandii* larvae parasitizing infected corn borer larvae (Andreadis, 1980). Van Essen and Anthony (1976) reported that *Notonecta undulata* (Say), a hemipteran predator of mosquitoes, became infected with *Nosema algerae* Vavra and Undeen after feeding on *Nosema*-infected larvae of *Anopheles quadrimaculatus* Say. York (1961) recovered dead *L. thompsoni* larvae containing microsporidian spores from corn borers infected with *N. pyrausta*. Although a positive identification of the microsporidium in the *L. thompsoni* larvae was not made, it is highly probable that it was *N. pyrausta*. This pathogen readily infects European corn borer larvae in Iowa and thus could be a cause of the small populations of *E. terebrans* and *M. grandii* and could have been involved in the disappearance of *L. thompsoni*.

Alternatively, the decline and disappearance of *L. thompsoni* could have resulted from a microsporidium pathogenic to the parasitoid but innocuous to the host. Such microsporidia are known. *Cardiobiles nigriceps* Viereck and *Campoletis sonorensis* (Cameron), hymenopterous parasitoids of the corn earworm, *Heliothis zea* (Boddie), and the tobacco budworm, *H. virescens* (Fabricius), are hosts to their own microsporidia, *Nosema campoletidis* Brooks and Cranford and *N. cardiobiles* Brooks and Cranford (Brooks and Cranford, 1972). Also, several Diptera, not necessarily parasitoids, are known hosts of microsporidia (Kramer, 1973; Sprague, 1977).

Because parasitoids are susceptible to the microsporidian pathogens of their hosts, it would be useful to assess the effect of all reported pathogens of the European corn borer on *E. terebrans*, *M. grandii*, and *L. thompsoni*.

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